ECOLOGICAL MONOGRAPHS

VOL. 5 JULY, 1935 NO. 3

OFFICIAL PUBLICATION OF THE

ECOLOGICAL SOCIETY OF AMERICA

CONTENTS

PUBLISHED QUARTERLY BY

THE DUKE UNIVERSITY PRESS

DURHAM, N. C., U.S.A.

ECOLOGICAL MONOGRAPHS

A QUARTERLY JOURNAL
FOR ALL PHASES OF BIOLOGY

Issued on the fifteenth of December, March, June, and September

The editorial board of this journal will consider ecological papers which are long enough to make twenty-five printed pages or more. Shorter ecological papers should be submitted to the editor of *Ecology,* which is also published by the Ecological Society of America. Both journals are open to ecological papers from all fields of biological science.

Manuscripts should be typewritten and may be sent to any member of the Editorial Board. Proof should be corrected immediately and returned to the Managing Editor at the address given above. Reprints should be ordered when proof is returned. Fifty copies, without covers, are supplied to authors free; covers and additional copies at cost. Correspondence concerning editorial matters should be sent to the Managing Editor; that concerning subscriptions, change of address, and back numbers to the Business Manager.

Subscription price, $6.00 per year. Parts of volumes can be supplied at the rates for single numbers, $1.50 each. Missing numbers will be supplied free when lost in the mails if written notice is received by the Business Manager within one month of date of issue. All remittances should be made payable to the Duke University Press.

Agents in Great Britain: The Cambridge University Press, Fetter Lane, London, E. C. 4. Prices can be had on application.

Entered as Second-class Matter at the Postoffice at Durham, North Carolina.

ECOLOGICAL MONOGRAPHS

VOL. 5 JULY, 1935 No. 3

SOME MARINE BIOTIC COMMUNITIES OF THE PACIFIC COAST OF NORTH AMERICA[1]

PART I. GENERAL SURVEY OF THE COMMUNITIES

By

V. E. SHELFORD
University of Illinois

A. O. WEESE
University of Oklahoma

LUCILE A. RICE
University of Illinois

D. I. RASMUSSEN
Utah Agr. and Mech. College

ARCHIE MACLEAN
Huntington Park (Calif.) High School

PART II. A STUDY OF THE COMMUNITIES OF A RESTRICTED AREA OF SOFT BOTTOM IN SAN JUAN CHANNEL

By

NETTIE M. WISMER
Lawrence (Kansas) Junior High School

and

JOHN H. SWANSON
Edinburg (Texas) College

[1] Contributions from the Zoological Laboratory of the University of Illinois, No. 467.

CONTENTS

Part I

General Survey of the Communities—Their Extent and Dynamics
The Major Communities

By V. E. Shelford

Dynamics and Extent of Bottom and Shore Communities

By Lucile Rice, D. I. Rasmussen, V. E. Shelford, A. O. Weese, Archie MacLean and H. C. Markus

Discussion

By V. E. Shelford

Part II

A Study of the Animal Communities of a Restricted Area of Soft Bottom in the San Juan Channel

By Nettie M. Wismer, Lawrence (Kansas) High School and John H. Swanson, Edinburgh College

PART I

GENERAL SURVEY OF THE COMMUNITIES—THEIR EXTENT AND DYNAMICS

THE MAJOR COMMUNITIES

By

V. E. SHELFORD

I. INTRODUCTION

In 1925, Shelford and Towler published a brief description of the marine communities near the Puget Sound Biological Station (now the Oceanographic Laboratories of the University of Washington). Data as to the physical and chemical conditions and the depth and bottom were summarized. This study considered about 75 km^2 of the 1000 km^2 covered in the investigations and reconnaissances which form the basis for the discussion in this paper. Our primary object in this monograph is to describe several new communities. One of them is a community of major or formational rank resembling those described by Petersen and colleagues ('11, etc.), and covers about one-fifth the sea bottom discussed. Its larger features were investigated in the summer of 1926, 1928 and 1930 by Shelford, while Weese undertook a special study of East Sound and Olga Bay in 1929. There was a sufficient overlapping of the stations of these two investigators to facilitate coöperation and comparison. This major community with its variations and subdivisions illuminates various important problems concerning the significance of physical factors and the reactions of organisms on the habitat.

As the investigation was extended to cover a larger area several subdivisions, and variations of the communities described in 1925, were discovered. The knowledge of dominant and influent animals, especially the motile forms, was extended and a revision of the lists of characteristic, uniformly distributed and important species was rendered necessary. The selection of representative species to illustrate general principles is difficult because of a lack of knowledge of habits and life histories and especially of variations in abundance from year to year. In a community such as the Strongylocentrotus-Argobuccinum biome,[2] briefly described in 1925, there are many important species. While a much longer list is presented here than in 1925, a still larger list would be desirable as many common forms receive no attention because they are not abundant or are not properly identified. The adequacy of the data for purposes of general discussion is, however, greatly extended over that of 1925.

[2] Biotic Formation.

The work of Weese on the faciations[3] of the new major community (Pandora-Yoldia biome) indicates the way in which physiographic processes may bring about a complete change in conditions and communities and thereby a complete change in fossilizable forms, the causes being entirely local and capable of taking place within a very short period. The work of MacLean carries the series of communities described by Weese farther toward the land climax of the region.

Rice's work on the Balanus-Littorina community serves a timely purpose of indicating the significance of the peculiar arrangement of individuals in various places. Her observations in southern California in 1931 although not presented in this paper served as a check on the observations of Rasmussen and those published by Shelford ('30). Observation on the tidal communities (Balanus-Littorina) at Barkley Sound (west shore of Vancouver Is.) has further illuminated the question of peculiar arrangements of species.

The actual investigations were supplemented by the general knowledge gained by dredging, bottom sampling, seining and clam digging, as well as other operations with classes of graduate students. Twenty or thirty graduate students were able to handle large amounts of material. This was done in a systematic and orderly way. For example, clams were dug on contour lines determined with a transit. The work was carried on in all cases with the aid of an assistant thoroughly familiar with the fauna. The discussion of the new Pandora-Yoldia biome and most of the other communities, is, however, primarily based upon investigations conducted for that purpose. The work of Wismer and Swanson (page 333) deals with the communities of soft bottom in a primarily hard bottom community area. While their work was done in coöperation with the other studies it constitutes a separate unit.

The communities are graded with reference to what are supposed to be the *largest community units* of the same or similar taxonomic composition. Since investigations have not as yet shown the extent of these larger units or their degree of fragmentation, the classification must be regarded as subject to revision, especially as regards leading dominants of uniform distribution throughout any major community (including its various fragments). The largest communities are distinguished by a *difference* in essentially *all* the species of abundance or dominance. The general plan of community classification adopted by American and British plant ecologists has been applied. Deviation from their familiar terms and usages are explained where such terms are used.

The experimental work of the writer and his associates, and life history studies of investigators at the station have been given community evaluation.

[3] The term faciation is applied to modification of the association resulting from the loss or the addition of a few of the important species.

This is limited, however, to studies concerned with species important in communities or studies having a general bearing upon the physiological differences between communities.

Two new methods were employed quite generally, especially in connection with the work on the new major community; the description of the implements used, particularly of a new quantitative net, is a further purpose of this paper. A much greater refinement in all the methods used as compared with the 1925 work has been possible in connection with the study of all the other communities of the area.

II. Area of Study, Methods and Communities

1. Area of Study

The area of study of the work of Shelford and Towler ('25) has been extended principally to the north and east. The northern boundary of the area which has been included in the investigations and reconnaissances is approximately 48° 48′ N. passing just north of the island of Patos. On the south, the southern end of Lopez Island, 48° 25′ N. is the boundary. The area is indicated in Fig. 1, and comprises approximately 1000 km^2, or 386 sq. mi. of water.

Approximately thirty-five dredging and bottom sampling stations were used and are indicated in Fig. 1 and 1a (nos. 51-85; 85 is shown on insert map). Stations 63 to 75 were intensively studied due to the presence of a series of communities hitherto undescribed, which occur on mud bottom in 3-75m of water in protected bays.

Other newly investigated bottoms were rock, sand, and mud in Rosario Straits, Barkley Sound, and Guemes and President Channels. Approximately 225 meters at Station 56 was the greatest depth reached with dredge or bottom sampler. For comparison a study was made by Shelford at Barkley Sound (west coast of Vancouver Island) covering several communities in some detail and significant reconnaissance of the shallow water bottom communities was also made. Use was made of observations on other parts of the Pacific Coast. On rocky shores between tide lines twenty-five stations indicated by a circle and arrow in Fig. 1 (1-25; 22-25 are shown on the insert map) were used for the study of barnacle-mussel communities. Fifteen stations were devoted to the study of bivalve-worm communities when exposed at low tide. They are indicated by a square and arrow in Fig. 1.

The general conditions in and about San Juan Islands were discussed by Shelford and Towler ('25). Since that date considerable investigation of the water from the chemical standpoint has been conducted by Thomas G. Thompson and his associates. Such studies include determinations of oxygen and salinity. Fig. 1 shows the salinity as indicated by isohalines. The map covers a larger area than the map already published (Shelford '30). The

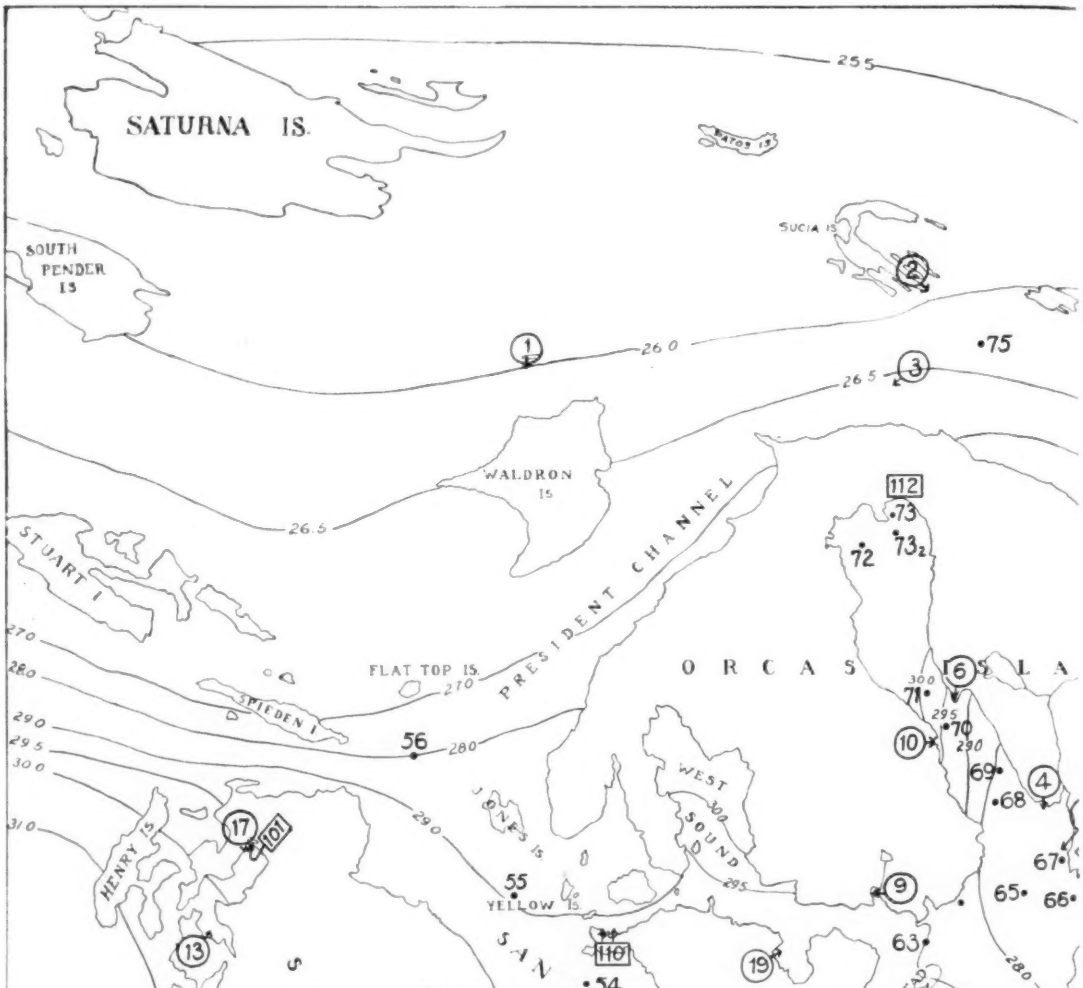

FIG. 1. Showing the estimated average relative summer salinity in grams of salts per liter, about the western half of the San Juan Islands and adjacent mainland and the location of stations. Dots = Dredging stations; Circles = Rocky shore stations; Rectangles = Sandy beach stations. The dot between 63 and 65 is station 64.

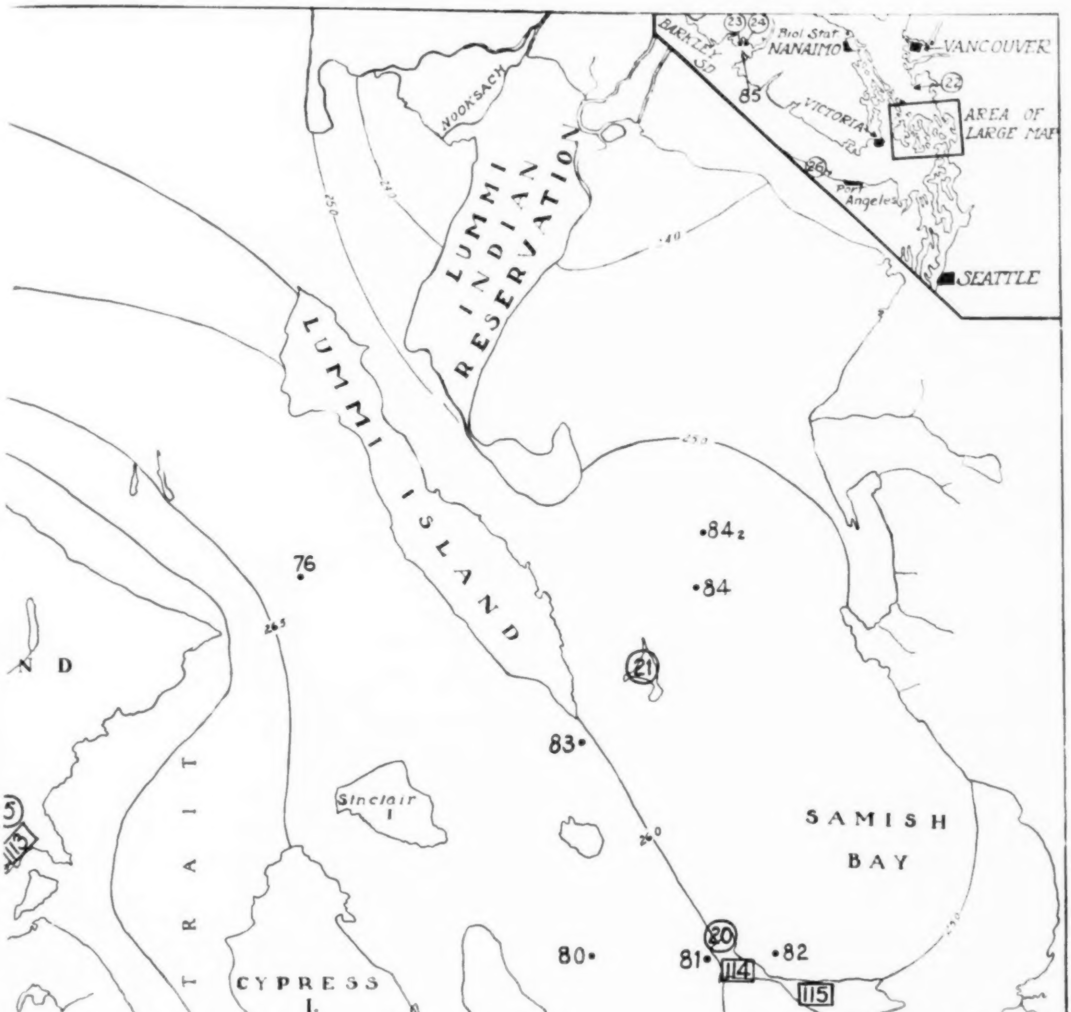

FIG. 1a. Same as Fig. 1; eastern half.

locations of the lines are based upon the shore communities and the proximity to rivers, as well as the published chemical work (Johnson and Thompson, '29; Powers, '20; Thompson, Lang and Anderson, '27; Thompson, Miller, Hitchings, Todd, '29).

A large series of determinations of alkalinity made in 1930 indicated that 80 or 90 parts per million is more nearly correct than 105 given by Shelford and Towler ('25). Powers and Logan ('25) and Powers and Hickman ('28) studied the carbon dioxide-carbonate relations of the sea water using a new method. The pH of the water is taken without contact with the air, then the water aerated with air, and a second reading taken. From these results it is possible to estimate the CO_2 pressure. Considerable work on light penetration into the water has been done since 1925. (Shelford and Gail, '22; Shelford, '29; and Williams, '29.)

2. METHODS

The Petersen bottom sampler was used almost exclusively, particularly in the studies of the communities in the waters about the southern portion of Orcas Island. A Sigsby trawl proved to be considerably more effective in securing fishes and other motile animals than the dredge.

A new quantitative net (Fig. 2) was used. It was designed by Dr. David H. Thompson of the Illinois Natural History Survey and proved to be very effective in securing small motile organisms. It was based upon the general principles of a casting net and was a cylindrical, conical topped net with numerous weights on the bottom ring. Modifications of the casting net consisted in providing an iron hoop to support the top of the net and a heavy central lead ring which tended to keep it on the bottom while the weights were being drawn together. See Fig. 2. The ring weight was released by a trip hook similar to that used on the Petersen bottom sampler. In Fig. 2 the net is shown in position for lowering. The net cylinder 4 ft. 6 in. high and 8 ft. in diameter hung from the hoop. The top was conical, the webbing reaching to the heavy weight ring. When the net was lowered into the water, the lead sinkers first rested on the bottom, then the hoop, finally the heavy ring. With the weight all released, the trip unhooked, leaving the weight ring resting on the bottom. When the rope to which the apparatus was attached was drawn up, the bottom of the cylinder net dragged over the sea floor to the central metal weight ring before the latter raised off the sea bottom. The bottom of the net was thus shirred together. While moving toward the center it dragged over the bottom and the animals resting there were forced to creep on top of it.

When it went straight down, this net covered 5 m^2 of bottom and in shirring together the bottom of the net dragged over less than 5m^2 as it often went down obliquely. The apparatus was therefore considered as covering

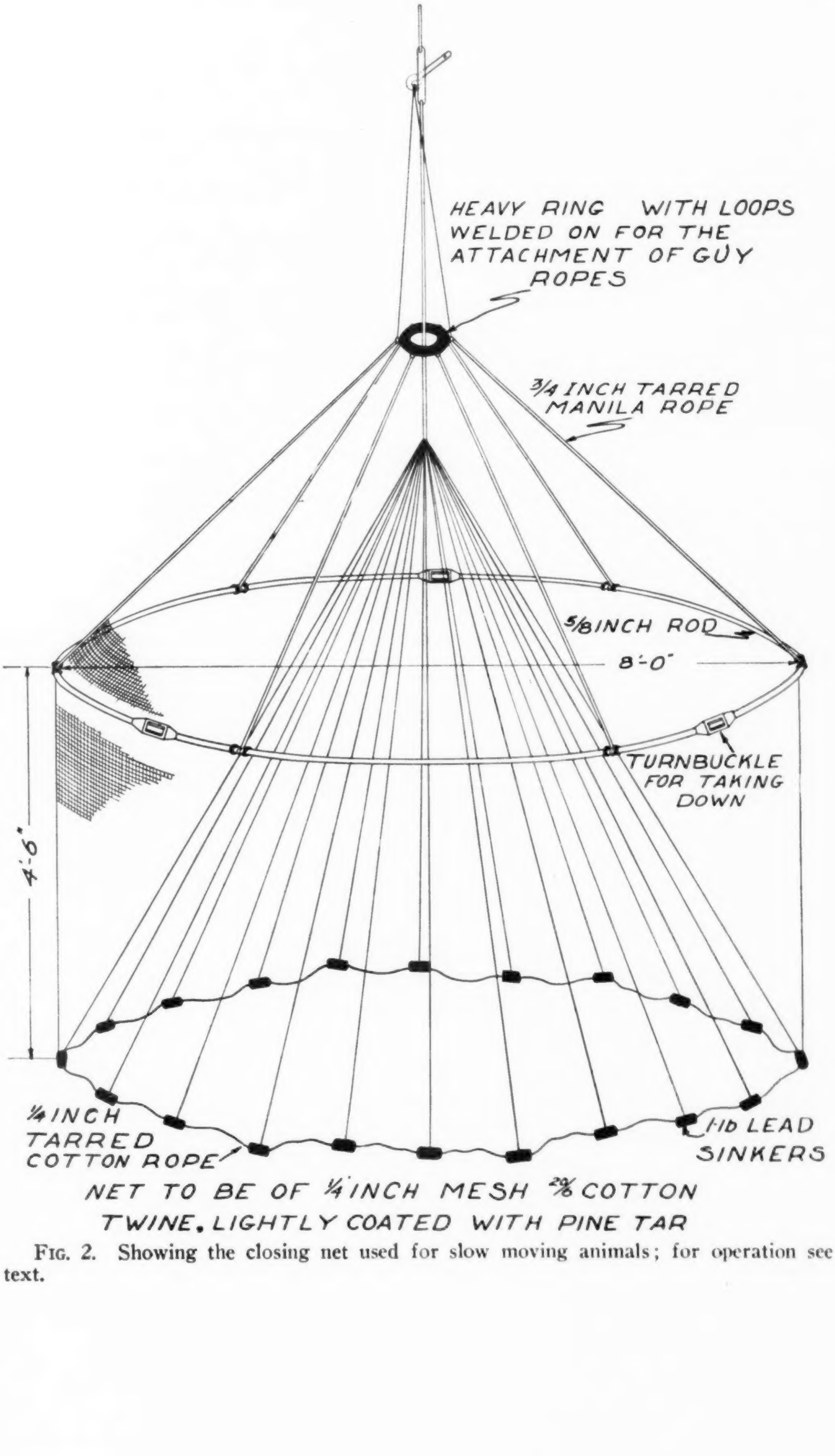

FIG. 2. Showing the closing net used for slow moving animals; for operation see text.

$4m^2$ of bottom. It was very effective in securing shrimps, crabs, and slow moving fishes. The difficulty with the net was the slowness with which it sank to the bottom and this difficulty was exaggerated by the necessity of using a very heavy cable attached to an awkward winch. In spite of these difficulties, however, it added very materially to knowledge of the communities studied. For the larger animals a net of much larger mesh and size would be necessary. The bottom rope must be very flexible or it could possibly be made of chain with small smooth links.

3. COMMUNITIES

The major communities[4] included in the area under consideration may be defined as follows:

III. Pelagic Communities

IV. Communities Associated with the Bottom (Figs. 3 and 4)

- A. Pandora-Yoldia Biome } Bivalve-annelid communities
- B. Macoma-Paphia Biome } Bivalve-annelid communities
- C. Strongylocentrotus-Argobuccinum Biome } Gastropod-barnacle communities
- D. Balanus-Littorina Biome } Gastropod-barnacle communities

All but the Pandora-Yoldia biome were mentioned in the earlier paper (Shelford and Towler '25). The map (Fig. 3) indicates the more important bottom communities of the area and their subdivisions. Their arrangement in a cross section between Bellevue Point on the northern half of the west coast of San Juan Island and South Bellingham, Washington, on the mainland is shown in Fig. 4. The land area is omitted. One of the communities indicated is a faciation of one of the associations of the Strongylocentrotus-Argobuccinum biome. It occurs along the shore just below low tide practically throughout the Pandora-Yoldia area, except off clam beaches.

III. Pelagic Communities (Murray and Hjort '12; Gran '12 and '31)

While none of the investigators concerned in this monograph have conducted intensive or quantitative investigations of this community, it is of such great importance in the modification of conditions surrounding other communities that a discussion of some of its features is essential. The pelagic community includes the plankton or floating organisms taken together with the swimming animals or nekton. The separation into those two groups as a basis for investigation has led to unfortunate failure to recognize the pelagic community proper. The density of population profoundly influences: (a) the penetration of light, (b) the food and chemical conditions in deeper water and at the bottom, and (c) the character of the bottom.

[4] A casual attempt (Shelford '16) with the advice of an algologist to use Forbes' Shore, Laminarian, and Coralline Zones which have no actual community basis was unfortunately copied in Pearse's Animal Ecology.

1. PLANKTON

It is not possible to agree with Allen ('21) and other algologists that diatoms of certain species are dominants or to refer to minute animals in similar terms. They do not take possession of the territory (*i.e.* volume) and hold it to the exclusion of other plants and animals. Their rôle is merely one of abundance of individuals and altogether weaker than is implied by "dominant." Diatoms, protozoa, etc., are the *vedomins*[5] of the pelagic community. Although selection may occur, the smaller planktonts are eaten by larger organisms with so little discrimination as to *species*, etc., that they serve a rôle similar to that of detritus and dissolved organic matter. The revival of interest in the latter has been stimulated recently by Krogh ('31).

Studies of the diatoms have been made by Gran *et al.* (Gran and Thompson, '30; Allen, '21-'29; Hutchinson, '28, '29; Cameron and Mounce, '22; Lucas and Hutchinson, '27; and Mounce, '22). Protozoa were studied by Eddy ('25); the Crustacea by Campbell ('29, '30), (also Lucas, '29; McMurrick, '16). Campbell ('29) found all types of smaller plankton organisms most abundant at a depth of about four meters. This included copepods, Peridinia, Tintinnidae, and diatoms.

On July 13, 1928, a series of eight water bottle samples were taken at depths of 1, 5, 10 and 20 m and 35, 50, 100 and 225 m at slack tide (station 56) over the Strongylocentrotus-Argobuccinum biome. Only twenty minutes intervened between the closing of the bottles in the two series. Counts of the diatoms by Dr. Gran showed that the maximum was at 20 meters. Diatoms were about 1/10 as abundant at the surface and 1/16 as abundant at 225 meters as at the maximum.

On the same date, over the Pandora-Yoldia biome (Fig. 1, station 69, see page 265), a series of four nearly simultaneous bottle collections (depths: —1, 5, 10, 20 m) in about 28 meters of water showed diatoms (counts by Dr. Gran) about 10 times as abundant as over the Strongylocentrotus community and the maximum was at 10 meters instead of 20 meters.

An examination of the animal plankton taken in nets hauled from the bottom to the surface within twenty minutes after each set of diatom collections just referred to, was made by J. C. Cross. The plankton over the Pandora-Yoldia community contained a few copepods, rotifers, and tintinnids, very many dinoflagellates, and various larval stages. That over the Strongylocentrotus-Argobuccinum community (see page 280) differed chiefly in the lack of dinoflagellates and in the presence of a greater variety of the larval stages. A few Sagittae were taken from the deep water here, but none over the Pandora-Yoldia community.

The only place where the larger animal plankton such as Crustacea,

[5] Professor Clements has proposed the use of *domin* for a weak type of dominance such as the larger pelagic animals exercise, and *vedomin*, meaning small domin, for the rôle of the minute planktonts.

FIG. 3. Provisional map of the communities of the sea bottom about San Juan Islands. The associations and faciations are shown in the first column of the legend and the biotic formations or biomes in the last.

In legend Fig. 3 for 'B.-M. californianus' read '*B.M.-edulis.*'
'B.-M. edulis' read '*B.M.-californianus.*'

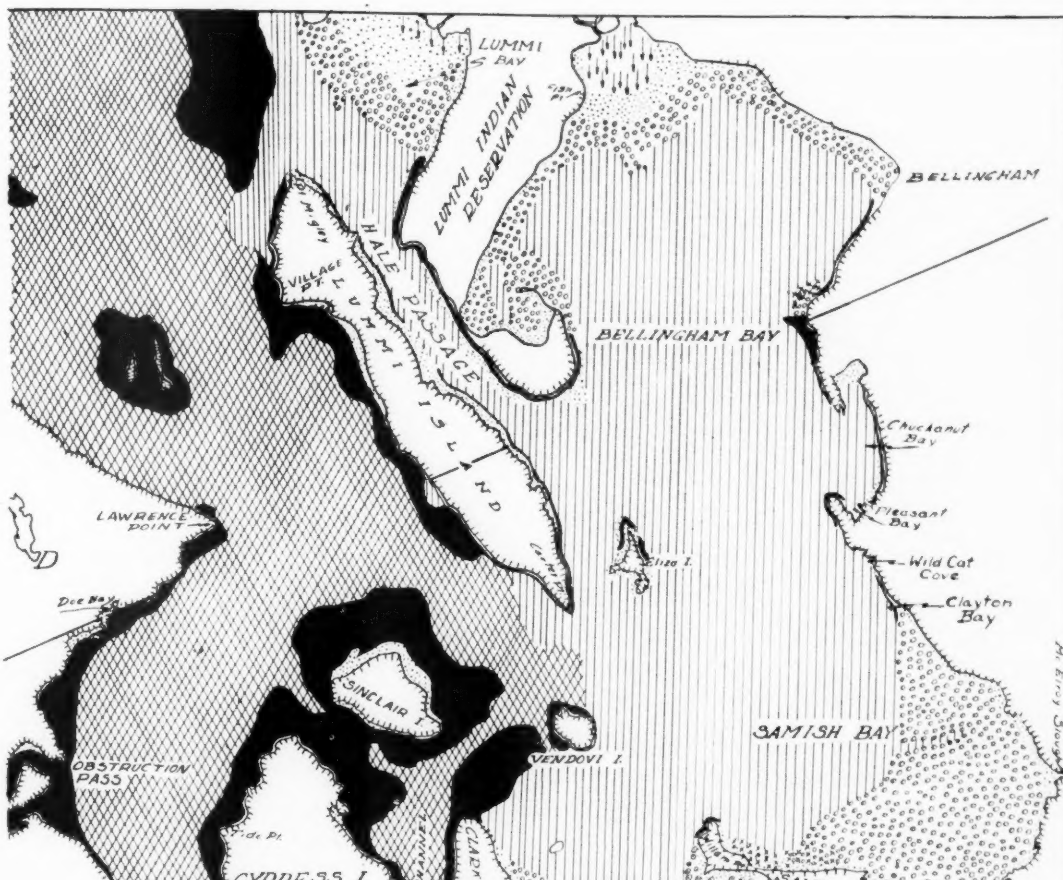

FIG. 3a. Same as Fig. 3; eastern half of the area.

Sagitta, etc., may be secured with certainty is on the south-west side of San Juan Island where salinity is highest (Fig. 1, station 57). These forms are either scarce or wanting or present only in deep water in San Juan Channel and waters nearer the mainland. This makes a distinct faciation in the waters near the mainland. Jellyfishes abundant during the summer months throughout both the inner and outer waters are: *Aequorea forskalea* P. and S., *Phialidium gregarium Haeck.* and *Thaumantias cellularia Haeck.* These together with less abundant species of Sarsia, Stomotoca, and Polyorchis and the common Ctenophores (Mnemiopsis and Pleurobrachia) make up a great part of the volume of the plankton of midsummer. There is a large seasonal element in the plankton, including many seasonal eggs and larval stages of various invertebrates and a few fishes (Bovard and Osterud, '18; Strong, '25).

2. NEKTON

The nekton or larger animals with effective swimming powers in this area consist largely of fishes and mammals.

(1) Pelagic Fishes (Kincaid, '19; Hubbs, '28)

The following have been taken more or less regularly and used in experimental work:

Clupea pallasii (Cuv. & Val.), herring (Shelford & Powers, '15; Shelford, '18; Powers, '21).

Hypomesus pretiosus (Girard), surf smelt (Shelford, '18).

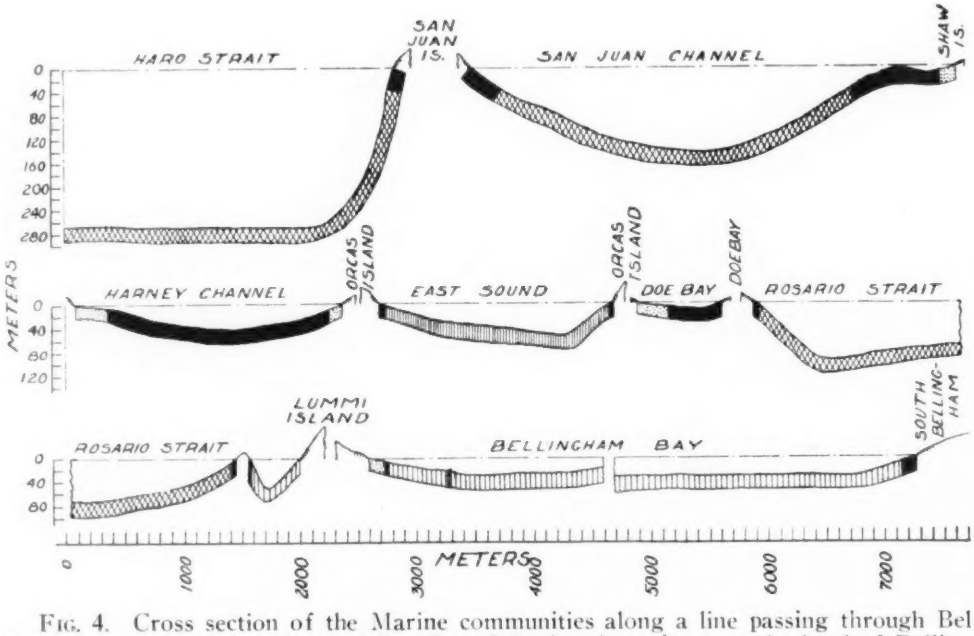

FIG. 4. Cross section of the Marine communities along a line passing through Bellevue Point on the west shore of San Juan Island and a point near the head of Bellingham Bay. The position of the line is indicated on Fig. 3-3a. The vertical scale is 5 times the horizontal; the legend is the same as in Fig. 3.

Thaleichthys pacificus (Richardson), eulachon.
Spirinchus starksi (Fisk), night surf smelt.
Allosmerus attenuatus (Lockington), white bait.
Oncorhynchus nerka (Walbaum), sockeye salmon; anadromous.
Oncorhynchus kisutch (Walbaum), silver salmon; anadromous (Powers, '21).
Oncorhynchus gorbuscha (Walbaum), hump-back salmon; anadromous (Shelford & Powers, '15).

(2) Pelagic Mammals

Orcinus rectipinna (Cope), killer whale.
Rhachianectes glaucus (Cope), gray whale.
Globicephala scammonii (Cope), Pacific blackfin.
Phocaena phocoena (Linnaeus), porpoise.

The killer (Orcinus) appears to be most abundant and was frequently seen in the San Juan Channel. In 1928 a school of killers came directly toward shore off Parker Reef, which rises abruptly from deeper water, at full speed until about 15 or 20 m off shore when they turned sharply to the left and avoided stranding. The blackfin was seen less frequently. The gray whales congregate in muddy bays and come to the surface daubed with bottom mud. In 1922 a light-colored whale (thought to be Rhachianectes) passed south between Brown Island and San Juan Island. Killers have been seen in the same location.

3. INTERACTIONS

Interactions are commonly divided into coactions or relations between organisms and reactions or effects upon the conditions of the habitat.

A. *Coactions* (Weaver and Clements, '29)

The coactions such as food relations are little known. The work of Lebour ('19 to '23) makes possible inferences as to the food of plankton animals and young fishes. The food of only a few adult fishes have been studied. The killer whale is known to feed upon fishes, salmon being mentioned especially (Scammon, '74), and also upon other whales. The same author states that the blackfish feeds upon squids and fishes.

B. *Reactions on the Habitat* (Clements, '05)

The plankton and other pelagic animals produce an important marine climatic reaction. They shut out much light from the waters below (Shelford and Gail, '22; Shelford, '29) and in sinking to the bottom at death consume much oxygen and produce carbon dioxide (Atkins, '22), sulphur compounds, and organic mud, having a profound effect upon bottom conditions, especially in quiet water.

4. PHYSIOLOGICAL CHARACTERS OF THE COMMUNITY

The independence of the bottom and shores is striking. Most of the work on physiological characters has been concerned with fishes. These are very sensitive to differences in the character of the water. Herring can recognize differences of 0.1°C. (Shelford and Powers, '14). These authors further showed that herring and salmon do not recognize differences in salinity but select their optimum hydrogen-ion concentration regardless of salinity. Powers ('21) confirmed this and followed the herring in its migrations in San Juan Channel. He found them closely associated with certain hydrogen-ion concentrations. Oxygen content and salinity appear to affect the reaction, however, and his findings as to exact pH do not hold good in other waters. Powers ('21) also studied juvenile salmon of two species with similar results. Rheotactic response of the sockeye is partially controlled by the oxygen content of the water (Daugherty and Altman, '25). Weese and Townsend ('21) showed that the jelly fish, Aequorea, moves downward when in contact with an adverse condition.

The resistance (Shelford, '18) of the herring and surf smelt *(Hypomesus pretiosus)* to CO_2 and other products resulting from adding small quantities of sulphuric acid (H_2SO_4) to the sea water was rated as 10 and 8 respectively while that of the viviparous perch, a shore vegetation inhabitant, had a resistance of 25. When sulphurous acid (H_2SO_3) was used in the same way the resistance of pelagic herring was rated 10; the viviparous perch from shore vegetation 21, and a bottom flounder 1100. H_2SO_3 may result from decomposition at the bottom. Other experiments by Shelford and Powers ('15) showed similar relations. We are justified in concluding that the pelagic fishes are much more affected by the condition of the water than shore and bottom species.

IV. COMMUNITIES ASSOCIATED WITH THE BOTTOM AND SHORE

These fall into two classes: (1) those dependent upon small water movements, much plankton, soft bottom of sand and mud (Pandora-Yoldia and Macoma-Paphia biomes) and (2) those on various relatively hard bottoms (Strongylocentrotus-Argobuccinum and Balanus-Littorina biomes) and much current or wave action. The first group is characterized by bivalve mollusks and annelids; the second by barnacles and gastropods. One of the latter, the Balanus-Littorina biome, has frequently been called inter-tidal, and the shoreward bivalve-annelid communities have been designated as "intertidal" also because a portion is exposed at low tides. This has led to much confusion and it is best to apply merely the term *tidal* to the Balanus-Littorina community and no other.

A. PANDORA-YOLDIA BIOME (A BIVALVE-ANNELID COMMUNITY)

In the discussion of the biome in general, mention is made of conditions and species which characterize the biome as a whole. Of necessity some of these are mentioned again in the discussion of its subdivisions. This biome approaches some of the communities described by Blegvad ('15-'30); Davis ('23-'25); Ford ('23); Hunt ('25); Jensen ('19); Petersen and Jensen ('11); and Petersen ('14-'18).

1. CONDITIONS

This community occurs on mud or soft bottom in 3 to 75 meters in Bellingham and Samish Bays, Padilla Bay, Lopez Sound, East Sound and much of the bay between Orcas Island on the north and Lopez and Blakely Islands on the south, including all of West Sound, North Passage, Deer Harbor, Echo Bay (in Sucia Island), and probably Reed Harbor and Hale Passage, though these have not been studied (Fig. 1, stations 63-73 and 80-84; Fig. 3).

The marine climatic conditions (Huntsman, '20) are quite different from those of other communities. The water is shallower, becomes warmer and produces many more diatoms. Tidal currents are weaker than in the San Juan Channel and the oxygen and salinity are usually or variably lower. The large amount of decomposition from the enormous production of diatoms is very great, yielding sulphur compounds and reducing the oxygen at the bottom. The small amount of oxygen could not be determined by the Winkler method in samples taken at the bottom because of the presence of sulphur compounds. Powers ('20) found the surface hydrogen ion concentration low as indicated by pH approximately 8.00. This is lower than over the Strongylocentrotus-Argobuccinum biome. The light is reduced greatly by diatoms. The usual scale of reduction down to 10 or 20 m. is crowded into 5 to 10 m. in this area (Shelford, '29, cf. Figs. 3 and 4a.). The community is best developed in areas of comparatively low salinity and high temperature with a large diatom population in summer. Attached algae are usually wanting or very few in number.

2. BIOME PREVALENTS OR PREDOMINANTS

A. *Dominants and Slow-Moving Influents*

Figures indicate the maximum and minimum of individuals per 10 m^2.

Pandora filosa Carp., asymmetrical bivalve; 20-350.

Yoldia limatula Say, yellow bivalve (Drew, '99); 1-541.

Marcia subdiaphana Carp., thin shelled clam; nearly always present, 1-90.

Sternaspis fossor Stimp., gooseberry worm; 10-460.

Amphicteis alaskensis Moore, worm; 1-100.

Phacoides tenuisculptus Carp., snail; 0-400.

Luidia foliolata Grube, starfish; common to abundant, 1-10.

Pycnopodia helianthoides (Brandt), 20 rayed star; 1-3.

B. *Influents*

Crago alaskensis (Lock.), shrimp; usually present, 1-20.
Lyconectes aleutensis Gilbert, red devil; common.
Crabs are few and not important. Hermit crabs are especially few.[6]

C. *Characteristic Species*

Cerebratulus montgomeryi Coe, large nemertean.
Dentalium rectius Carp., tooth shell.
Yoldia thraciaeformis Storer, large Yoldia.

These species are distributed throughout the biome and constitute the binding dominants and influents. The biome is divisible, however, into two or possibly three associations which include these dominants and along with them others of restricted range. The associations recognized are the Cucumaria-Scalibregma association, the Clymenella-Yoldia association and the Diopatra-Chelyosoma community, which covers a very small area and is here considered as representing an ecotone rather than a distinct association. This status is provisional and may be changed when other examples have been discovered and studied.

3. ASSOCIATIONS

A. *Cucumaria-Scalibregma Association*

(1) Conditions.

The bottom consists of mud composed of fine silt, much of which is quartz, mixed with organic detritus, especially diatom detritus in various stages of decomposition (Jensen, '14). An examination of the bottom sediment in East Sound was made on August 7, 1928, about one kilometer into the Sound. The fresh part of this sediment was 5 cm. deep, down to the darker mud of the year before. The upper part consisted of plankton detritus, other plant and animal material and a small amount of fine transparent sand with grains of various shapes and sizes. The amount of this sand increased in the deeper parts but organic detritus still equaled or exceeded the sand in volume. These fine quartz particles were nearly always in evidence under the microscope in the plankton collections secured with a tow net from San Juan Channel. The principal sources of this material are the Fraser and Nooksack rivers. The character of the bottom is similar throughout, though the amount of organic material appears to increase toward the upper end of East Sound (Weese, page 310).

It has already been noted that the oxygen content of the Puget Sound water is always about 1 cc. per 1 below saturation for pure sea water. The oxygen at the sea bottom in these waters is generally very low and the iodine

[6] *Nucula castrensis* Hinds, camp nut shell, is local and usually on the border of the community where it meets the Strongylocentrotus-Argobuccinum community; also in mud pockets in the S. A. community.

absorption of samples so great that the small amount of iodine liberated by the Winkler method is quickly, if not immediately, absorbed, rendering its determination unusually difficult. The oxygen content usually decreases from the surface toward the bottom. The carbon dioxide content is doubtless high and other products of decomposition such as hydrogen sulphide, etc., are very important.

The diatom plankton of this area is frequently extremely dense (Gran and Thompson, '30) especially in East Sound. The enormous phytoplankton production about the mouth of the Fraser River appears to supply some diatoms (Lucas and Hutchinson, '27) which appear to drift in from the Rosario Strait. Many are produced locally under the stimulus of high temperature. Their density is so great as to transmit only 2% of the violet, blue, green, and yellow light (average of the four colors) to 8 m, while in the clearer water of the San Juan Channel, 13% is transmitted to 8 m. This phytoplankton has a pronounced effect upon the conditions at the bottom not merely in producing deritus but in modifying light (Shelford, '29) with a very marked effect upon the character and success of the life at and just above the bottom.

(2) Dominants and slow-moving Influents.

The expanding worm (Scalibregma) is very important and has increased in importance during the period in which the community has been observed. It occurs in the Danish waters and is a pure detritus eater (Blegvad, '14, p. 60). The white cucumber, *Cucumaria populifera* (Stimp.), is very abundant also and is probably a pure detritus eater; as is also the larger spotted cucumber, *Cucumaria piperata* (Stimp.), which is confined to the shallower water. The biome prevalents listed on page 265 occur mixed with the species characteristic of the association. Figures indicate the maximum and minimum number of individuals per 10 m^2.

Scalibregma inflatum Rathke, expanding worm; 1-9600.
Cucumaria populifera (Stimp.) Theel, white cucumber; 1000-8000.
Luidia foliolata Grube, fragile starfish; 1-10.
Pycnopodia helianthoides Brandt, 20 rayed starfish; ½-1.
Yoldia limatula Say, yellow bivalve; a detritus eater (Drew, '99); 10-500.
Pandora filosa Carp., asymmetrical bivalve, a detritus eater; 10-300.
Ophiopholis aculeata var. *kennerlyi* (Lyman), brittle star; usually present.
Amphiodia occidentalis (Lyman), brittle star; abundant 1926.

(3) Influents.

Crago dalli (Rath.) shrimp; 1-48, 1926.
Neomysis kadiakensis Ort., shrimp; abundant in 1930 circular net catches.
Lycodes brevipes Bean, short finned eel-pout; present 1926, 1928, 1930.

Lycodopsis pacificus (Coll.), Pacific eel-pout; present 1926, 1928, 1930.
Psettichthys melanostictus Gir., black spotted flounder; present 1926, 1928.
Porichthys notatus Gir., midshipman; 1926, 1928.

(4) Characteristic species.

Serripes groenlandicus Beck., brilliant bivalve, very few.
Corolla spectabilis Dall., sea angel; few.

The existing knowledge concerning the interactions and other dynamic features of Pandora-Yoldia biome is based on this association. However, this is discussed in general terms on page 271 following the description of the association and the noteworthy variations within them. These have been termed faciations.

(5) Faciations.

In the area occupied by the association in typical composition, are included much of Deer Harbor, West Sound, Olga Bay, the outer third of East Sound and probably Lopez Sound. Throughout this area in water from three to six meters around the shore, there is a faciation characterized by *Cucumaria piperata* (Stimp.) which largely takes the place of *Cucumaria populifera* (Stimp.) and is frequently accompanied by tunicates. This may be designated as the Scalibregma-C. piperata faciation. The three other faciations of this association are described by Weese (page 310). These occur in the inner part of East Sound and presumably exist in West Sound and elsewhere. Those studied occur in waters more saline than those of San Juan Channel. They are in part due to the loss of prevalent species and in part due to the addition of other species of importance.

B. *Clymenella-Yoldia Association*

This association was not investigated with the bottom sampler, but merely by reconnaissance dredging. Only a few general points can be brought out regarding the bottom and other conditions. It is found in Bellingham and Samish Bays and adjacent waters.

(1) Conditions.

The bottom is soft oozy mud, and contains more terrigenous matter than the bottom associated with the Cucumaria-Scalibregma association, and has a slightly yellowish color. The difference in taxonomic composition of this association as compared with the preceding one is very striking, principally on account of the very large number of worms of the genus Clymenella. The biome prevalents listed on page 256 occur mixed with those listed below.

(2) Dominants and slow-moving Influents.

Clymenella rubrocincta John., bamboo worm; very abundant.
Dendronotus giganteus O'Don. giant nudibranch; abundant.

Yoldia ensifera Dall, yoldia; common.
Scalibregma inflatum Rathke, expanding worm; few.
Glycera sp., worm; few.
Nucula linki Dall, bivalve; common.
Glycinde armigera Moore, annelid.
Pandora filosa Carp., asymmetrical bivalve; present.
Luidia foliolata Grube, fragile starfish; common.
Amphitrite robusta John., terebellid worm.
Crago franciscorum (Stimp.), Frisco shrimp; common.
Polinices groenlandica (Beck) Möll., moon snail.
Amphiodia urtica (Lyman), brittle star.

(3) Influents.

This class appears few both in species and number, in part due to our failure to investigate the fishes.

Crago alaskensis (Lock.), shrimp.
Crago communis (Rathbun), shrimp.
Hyas lyratus Dana, crab; few.

The *faciations* of this community have not been studied. No experimental work has been conducted on its characteristic animals.

4. EXTENT, RANK AND BOUNDARIES

The extent of this biome is quite unknown but the boundaries of the portion studied are sharp and ecotones are narrow. The definite habitat (hydrographic) conditions which it requires, are to be found in numerous inlets along the Pacific coast of North America. The distribution of the dominants and slow moving influents as given in economic and taxonomic literature indicates a considerable range both into Alaskan and into Southern Californian waters. This literature is an unreliable and even a treacherous guide, but usually species are important community constituents over half at least their range.[7] It seems best to consider the small area studied as a disconnected portion of a much fragmented biome, probably widely distributed in protected inlets.

A. *Ecotone Communities*

Diopatra-Chelysoma ecotone between Pandora-Yoldia and Strongylocentrotus-Argobuccinum biomes. This occurs between Upright Head and Foster Point, in the eastern portion of Harney Channel in depths of 50 to 75 m.

The bottom is of soft mud, but somewhat denser than in the shallower bottoms, due to the terrigenous materials from adjacent rivers. There is

[7] There are many examples of the failure of such distribution records. In primeval times the white pine, for example, occurred in scattered, insignificant patches and as single trees over twice as much territory as it occurred as a general dominant.

much less plankton detritus and fresh organic matter. The circulation at the bottom presumably is greater than in the other situations.

This community covers such a small area that while it is fairly distinct it is best to leave the determination of its status until such a time as further examples have been found. Since the character is in part a matter of depth, there is little bottom in the region of study which could be expected to have this type of community. While a considerable number of forms occur, which belong properly to the Strongylocentrotus-Argobuccinum biome, notably *Pecten hericius* Gould and the crabs, Cancer and Oregonia, it lacks several characteristic species found on similar bottoms in the Strongylocentrotus-Argobuccinum areas. *Modiolus modiolus* Linné is essentially wanting here. Green sea urchins rarely occur. Some of the fishes of the Strongylocentrotus area are occasionally present.

(1) The following are the chief dominants and slow moving Influents.

Figures indicate the maximum and minimum number of individuals per 10 m^2.

Diopatra californica Moore, ornamented tube worm; 125-200.
Chelyosoma productum (Stim.), flat topped tunicate; 5-100.
Marcia subdiaphana Carp., thin shelled bivalve; 10-150.
Styela gibbsii (Stim.), tunicate; 1-20.
Large sea anemones, a few always taken.
Pectinaria brevicoma John., sand tube worm; 1-30.
Pycnopodia helianthoides (Brandt), 20 rayed star; 1-2.
Nucula castrensis Hinds, truncated bivalve; 1-40.
Phyllochaetopterus sp., bamboo tube secretor; 20-60.
Ophiura sarsii Lütk., brittle star; usually present.
Pecten islandicus Muell., scallop; 2-8.

(2) Influents.

Ronquilus jordani (Gilbert), Jordan's ronquil; present 1928.
Porichthys notatus (Girard), midshipman; 1928.
Lycodopsis pacificus (Coll.), Pacific eel-pout; 1930.

(3) Characteristic Species.

Cardium ciliatum Fabr., small cockle.

B. *Shallow Water Ecotone Communities*

The shallow water ecotone community lying between the Pandora-Yoldia biome and the Strongylocentrotus-Argobuccinum biome is characterized by various tunicates. These are *Chelyosoma productum* (Stim.), the flat top tunicate, *Styela gibbsii* (Stim.), and *Pyura haustor* (Stim.). Large red sea anemones are common as in the deeper water ecotone. *Trichotropis cancellata* Hinds occurs among the Pandora-Yoldia species.

Where the shore is sandy there is an ecotone between the Pandora-Yoldia

biome and the Macoma-Paphia biome, characterized by the presence of Paphia, *Macoma inquinata* Deshayes, hermit crabs, flat fishes, etc.

5. INTERACTIONS

The worms, sea cucumbers, and bivalve mollusca probably feed heavily on the detritus at the bottom while the starfishes feed upon the bivalves and cucumbers. The large size and considerable numbers of the starfishes should make them potent influents upon the more stationary members of the community. Fishes probably take as heavy toll of the sedentary types as do the starfishes (Stevens, '30).

The reaction of the pelagic community, on the bottom is very marked as regards lights, etc., and has been pointed out. The numerous burrowing worms and mollusks tend to bury and consolidate the organic matter with the terrigenous deposits (Moore, '31).

6. ANNUATION

There were many variations in numbers of individuals per unit area and in species present between 1926 and 1930. Table 1 shows these relations.

TABLE 1. Showing the variation in numbers of several invertebrates per 10 m^2 in the Pandora-Yoldia biome. X indicates presence in very small numbers. The location of stations is shown on Fig. 1, page 254.

Species	Station	1926	1928	1930
Yoldia limatula Say and *Yoldia ensifera* Dall	63	200	360	25
	64	541	200	10
	67	X	X	16
Pandora filosa Carp.	63	X	X	X
	64	350	100	120
	67	40	30	20
Marcia subdiaphana Carp.	63	90	70	13
	64	16	15	0
	67	20	30	20
Scalibregma inflatum Rathke	63	0	X	300
	64	0	X	320
	67	950	X	1820
	68	X	1350	9610

7. LIFE HISTORIES AND PHYSIOLOGICAL CHARACTERS

The Mollusca of this community have apparently not been studied locally. In a similar community in the Danish waters (Jensen '19), studied growth rings showing periods of growth in important Mollusca covering from two to nine years. Blegvad ('28) indicates that some of the Mollusca of the Danish community (e.g. *Abra alba*) do not live beyond the second summer. The life histories of the animals without hard skeletons are not known. Little

physiological work has been done. The black spotted flounder which is found in this community was found by the writer (1918) to be a hundred times as resistant to H_2SO_3 and fifteen times as resistant to CO_2 as the herring. This is in keeping with its ability to live on decomposition-laden bottoms.

8. COMPARISON WITH DANISH COMMUNITIES

The activities, reactions, and food habits of the animals of this biome have not been studied. The same is true of physiological responses; this was due chiefly to the distance from the biological station. Blegvad ('14) made extensive studies of similar communities in Danish waters, including studies of the food habits of a few of the Pacific species. None of these have comparable significance in both the Danish and Puget Sound waters but the comparisons suggested in Table 2 and 3 are important.

TABLE 2. Species common to the Danish and Puget Sound Waters (Blegvad, '14, '16).

	Abundance		Blegvad's Classification as to food habit
	Danish	Puget Sound	
Scalibregma inflatum Rath	Relatively few	Very abundant	Detritus eater
Ophophiolis aculeata (Linn.) Gray	Abundant	Few	Carnivorous detritus eater

TABLE 3. The following species belong to the same genera as those discussed for the Danish waters and probably have similar habits (Blegvad, '14, '16).

Puget Sound species	Food habits of species of the same genus in the Danish waters
Dendronotus giganteus O'Don.	Carnivorous detritus eater
Glycera sp.	Carnivore
Nephthys coeca Fabr.	Carnivore
Lubrinereis bicirratus Tread.	Carnivore
Dentalium rectius Carp.	Carnivorous detritus eater
Macoma expansa Carp.	Detritus eater
Polinices groenlandica (Beck) Moll.	Purely carnivorous
Nucula linki Dall.	Detritus eater
Styela gibsii (Stimp.)	Detritus eater
Marcia subdiaphana Carp.	Detritus eater
Cucumaria populifera (Stimp.)	Detritus eater
Cucumaria piperata (Stimp.)	Detritus eater
Crago alaskensis (Lock.)	Carnivorous detritus eater
Crago communis (Rathb.)	Carnivorous detritus eater

B. MACOMA-PAPHIA BIOME (AN ANNELID-WORM COMMUNITY)

1. LIFE FORMS AND CONDITIONS

The life forms of this community resemble those of the Pandora-Yoldia biome. Bivalves and worms are important and starfishes and flatfishes occur. The native bivalves of the Macoma community usually are not abundant

beyond about 1m *above* mean low tide and usually are very scarce above 1½m. However, this distribution is greatly modified by the water-holding capacity of the soil or bottom materials. The habitat is covered with sea water at its upper edge about 60 per cent of the time (Shelford and Towler, '25, page 46) and the beach materials usually hold water in quantity while the tide is out.

In the work of Shelford and Towler ('25) this community was not investigated or understood below low tide line. Petersen has pointed out that *Macoma balthica* Linn. and *Mya arenaria* Linn. (the latter introduced in the Pacific) are important dominants in the similar biome in the Baltic and the coastal waters of northern Europe and extend down to 20 or 30 m. in a few places. He believes that this community is restricted to shallow water because of the destruction of young stages by echinoderms.

The climate of this community varies from that of the Strongylocentrotus-Argobuccinum biome in quiet bays to that of the Pandora-Yoldia biome. The influence of the substratum here is of greatest significance in shallow water and is concerned with its water holding capacity while the tide is withdrawn. Bruce ('28) has made a study of this property of beach sands. The community is highest up on the beaches with finest sand of greatest water holding capacity. A comparable community disappears quite completely above the low water mark on open shores of the Pacific. Fraser and Smith ('28) state that "the position in relation to tidal currents and exposure or protection from storms has much more to do with the rate of growth of clams than the actual composition of the beach." Smith ('28) found growth correlated with quantity of plankton.

The dominant clams find optimum conditions, as indicated by abundance at different levels, between one and ten meters below high tide. The maxima differ in position for the different species, on different shores and beaches and in different years. In some years there is a definite order among the species; in others considerable irregularity occurs. Quite frequently maxima occur at two or more levels, often explainable on the basis of water holding capacity of the sand. Not infrequently *Macoma nasuta* and *M. secta* are at a maximum at about the mean of the lowest 6 or 8 tides of each month.

Wismer and Swanson (p. 340) found more of the clams at about 9 or 10m than at 3m below high tide. Most of the dominants are found at a depth of 10m. *Cardium corbis* occurs at the lower limit of the community. Paphia staminea is distributed to a considerable depth, perhaps as much as 100m in very small numbers. It is alleged to show shell modifications which distinguish deep and shallow water individuals. The greatest area of the community and the greatest total number of individuals is subtidal; the remainder are bathed in the waters held by the beach during low tide. The community is essentially subtidal.

The introduced *Mya arenaria* ordinarily is found higher on beaches than any of the native species, and *Macoma nasuta* and *Macoma balthica* are found highest of the common native species. *Tellina carpenteri* Dall which occurs in only a few places is found as high as Mya. Crabs of the family Pinnotheridae are common in clams and in Upogebia holes.

2. BIOME PREVALENTS OR PREDOMINANTS

A. *Dominants and Slow-Moving Influents*

The figures indicate the maximum and minimum number of individuals per $10m^2$ at the point of maximum abundance on the beach. Those showing 0 are sometimes wanting on a particular beach.

Macoma nasuta Con., bent-nosed clam; 5-250.
Macoma secta Con., clam; 10-150.
Macoma inquinata Desh., clam; 20-250.
Paphia staminea Con., little-neck clam; 0-200.
Macoma balthica Lin., pink clam; 0-500.
Saxidomus giganteus Desh., clam; 0-30.
Cardium corbis Mart., cockle; 1-10.
Schizothaerus nuttallii, Con., giant clam, Washington clam or horse clam; local.
Nereis virens Sars., and other nereid worms; 4-140.

B. *Influents*

(1) With preference for open sandy areas.
Lepidopsetta bilineata (Ayres), sole.
Oligocottus maculosis Gir., tide pool sculpin; very common.
Psettichthys melanostictus Gir., black spotted flounder.
Platichthys stellatus rugosus Gir., starry flounder.
Liparis fucensis Gir., rock sucker.
Hemigrapsus oregonensis (Dana), hairy shore crab.

(2) With preference for eel grass (Zostera).
Cancer productus Rand., edible crab; common.
Cancer magister Dana, edible crab; common.
Telmessus cheiragonus (Tilesius), helmet crab; common.
Sebastodes maliger J. & G., rock fish.
Sebastodes caurinus (Richardson), yellow spotted rock-fish.
Sebastodes melanops (Gir.), rock fish.
Pholis ornatus (Gir.), green or chameleon blenny.
Pholis lactus (Cope), green or chameleon blenny.
Syngnathus griseolineatus Ayres, pipe fish.
Lumpenus anguillaris (Pallas), snake blenny.
Gasterosteus aculeatus aculeatus Lin., Alaska stickleback.

Pagurus granosimanus (Stimp.), hermit crab; see Wismer and Swanson, p. 342.

Pagurus beringanus (Bened.), hermit crab; see Wismer and Swanson, p. 342.

Pallasina aix Starks., Pallas' sea poacher.

Ophiodon elongatus Gir., ling cod., juvenile.

3. ASSOCIATIONS

The study of this community has not been adequate for the detailed mapping and interpretation of the associations. In the work of 1922 and 1924 (Shelford and Towler, '25) two associations were recognized. These are, however, to be regarded as purely provisional.

A. *The Macoma-Paphia Association*

In addition to the prevalents listed on page 274 this association is characterized by the bivalves of these genera with Saxidomus and Schizothaerus and abundant nereid worms; it is in the more protected waters. There is no doubt but that a community of this composition quite generally occupies the smaller beaches among the San Juan Islands. Succession with physiographic change due to cliff erosion has been discussed by Wilson ('26).

B. *The Macoma-Leptosynapta Association*

This association occurs on the more exposed shores and evidently on the wide flat areas with Zostera such as False Bay and possibly some of the flats north of Samish Island and near Anacortes. Schizothaerus and Saxidomus are often wanting and *Paphia staminea* is far from abundant, while *Cardium corbis* is usually more prominent than in the other association. *Arenicola claperedii* Lev., smooth clam worm and *Tellina carpenteri* Dall, bivalve, and *Leptosynapta inhaerens* are characteristic of the community at False Bay (stations 102 and 103).

A reconnaissance on both sides of Samish Island (stations 114 and 115) where Zostera is abundant showed the usual assemblage of animals. *Cardium corbis* was conspicuous. *Saxidomus giganteus* was present and *Macoma nasuta* was fairly abundant but decreased with depth of water. A few *Paphia staminea* were found and young fishes were observed in the more open spaces among the eel grass. Sand dollars, *Dendraster excentricus* Esch. occur in two places (near mainland; records by Prof. T. Kincaid) and the conditions appear similar to the smaller area in False Bay. The coast north of Anacortes appears to resemble the great beds of Zostera described by the workers of the Danish Biological Station (Petersen, '11; Blegvad, '14). The detritus from these is of the utmost importance as the food of invertebrates which serve as food to the fishes. Because of the presence of sand dollars

which characterize a faciation these areas are suggested as in part at least of a composition similar to that of False Bay which has been provisionally designated Macoma-Leptosynapta association.

4. FACIATIONS

A. *Ulva Faciations*

The Ulva "association" of Muenscher ('15) lies in shallow water, frequently at least on the shoreward side of the Zostera. Ulva grows on the beach up to a point which is somewhat above mean low water, though its upper limit appears to vary from year to year. It often covers beaches more or less completely and increases their water holding capacity while the tide is out. Some of the plants appear to be detached and fragments of plants are common. It is often an important factor on beaches. It does not suppress the animal dominants common on the open sand areas which the Macoma-Paphia biome occupies.

In the quieter small bays and recesses of the shore, Ulva and a few other algae commonly grow among the eel grass. Here, however, only occasionally does it become a codominant associated with eel grass (*Zostera marina* Linn, and other species); (Muenscher, '15).

B. *Zostera Faciations*

Zostera marina L., eel grass, occurs in both the provisionally suggested associations, Macoma-Paphia and Macoma-Leptosynapta, but limited investigation renders detailed discussion impracticable. Eel grass is not uniformly distributed in either association. There are many local areas of eel grass but the large areas are near the mainland. These lies northeast of Samish and northeast of Fidalgo Islands and contain about 65 km^2 (26 sq. mi.). Zostera introduces an additional layer into the community by supporting several attached algae, especially Porphyra and sometimes Ulva and Enteromorpha, and the filamentous diatoms. These epiphytic plants increase the surface and hiding places so that the Zostera area supports more animals than it would otherwise. *Lacuna porrecta* Carp. is usually present; large amphipods unidentified; *Caprella* sp.; *Pentidotea resecata* (Stimp.), isopod; *Epiactis prolifera* Ver., sea anemone; and *Haminoea vesicula* (Gld.) occur, often in abundance (station 102). Lacuna does not occur on eel grass at a distance from rocks and kelp. The nearer these are the greater Lacuna's abundance. The same is true of the isopods. The sea anemone and the Haminoea are most abundant on muddy bottoms where there is evidence of succession toward land (near station 107). Sometimes there are many shrimps and crabs in the eel grass and at other times few or none are found. Young fishes are also sometimes abundant. All the motile forms appear to move in and out of the vegetation. European workers have shown that this

faciation is a very important feeding area for young cod, eel, plaice dab, flounder, etc. These relations have not been worked out for Puget Sound but eel grass areas may well be of great value to fisheries.

c. *Dendraster Faciations*

The sand dollar, *Dendraster excentricus* Esch., is abundant locally among the eel grass and is the only one of a series of characteristic forms in False Bay (station 103) known to be found locally in the large areas of eel grass of the flats near Fidalgo and Samish islands.

This striking addition to the usual community composition may entitle these areas to be ranked as sand dollar faciations though their local character may make them more properly termed lociations.

The Macoma-Paphia biome undoubtedly represents an important climax though much study of its development (succession) on new areas as well as much geographical and annual study would be necessary to interpret the series of associations, faciations, etc., included in the community.

5. EXTENT, RANK, AND BOUNDARIES

This community occurs in fragments in the areas of study and in general is characteristic of protected bays just as is the *Macoma (balthica)*-Mya community of Europe. The fragments of the biome taken together would cover a considerable area though its depth is slight. No evidence has yet been found for the community's extension to depths beyond the 8-10m below low tide. The range of bottom materials which it inhabits is great, including organic muck, finest silt, sand and fine gravel. The community is evidently wanting on open shores and bays facing the Pacific Ocean (Edmonson, '20).

6. INTERACTIONS

A. *Coactions*

Blegvad ('16) worked on the coactions in the Macoma-Mya community of the western European waters. He found that the bivalves of the portion of this community toward shore from the Zostera faciation were not eaten by fishes and thus grew to great size. This corresponds to the area from which clams are commonly dug on the shores of northern Oregon, Washington, and British Columbia. In the plant belt Blegvad found that the fishes feed on juvenile bivalves. There are also many food, shelter, and attachment coactions between the Zostera, the attached algae, and attached animals; also between the attached animals and the small and juvenile fishes which frequent the plants. Outside the Zostera faciation in the Danish waters where the bottom materials are finer the large food fishes devour the various bivalves and worms. The same is probably true about the San Juan Islands; the deeper water yields small specimens of the dominant bivalves. In our

area the flatfishes are sometimes on the shoreward side of the Zostera at high tide and may take food from the area; especially the young flatfishes are common here and may take juvenile bivalves. This subject should be studied in the interest of fisheries.

B. *Reactions*

All the community constituents react on the habitat but wherever it grows, Zostera is most important. It checks currents and wave action, produces shade and tends to hold the bottom materials. Fishes, bivalves and gasteropods move the bottom materials at the surface and the worms pass quantities of soil through their alimentary tracts. Upogebia is said to have completed the ruin of over-fished Pacific oyster beds. The native oyster bed is evidently a climax community (Stevens, '26, p. 348).

7. COMMUNITY DEVELOPMENT

Opportunity to study succession on new deposits not accompanied by low salinity, as about the mouths of rivers, are rare. One case not fully taken advantage of, near Friday Harbor, was studied enough to show that the investigation of quasinatural areas must be supplemented by actual experimental operations. The gravel deposit in the moraine which forms the south end of San Juan Island was utilized commercially on a large scale for two or three years ending in December, 1928. The gravel was run down a chute and over sorting screens into barges. This gave a large residue of the finer material which found its way onto the adjacent bottom. This deposition of quantities of silt reached a depth of 30 cm. or more at 500 feet from the barge loading point within a short time. The material from the line of chutes and screens produced a long peninsula which formed a small bay deeply silted with fine material which came from the gravel.

No examination of the community was made at the time operation stopped. Twenty months after the operation of the pit ceased, S. W. Howe made a careful census of animals of the area. The silt originating from the gravel was 50 cm. deep as a result of two or three years operation. Worms were plentiful. *Macoma nasuta, M. inquinata, M. identata, Paphia staminea,* and *Cardium corbis* were found. Total clams ranged from 10 to 84 per m^2. The life history of *Paphia staminea* has been worked out by Fraser and Smith ('28). This clam spawns in summer and thus the 1929 clams should be only a year old and about two-fifths of an inch long. Since the clams were much larger than this it became evident that they had survived the rapid silting and that some additional experimental method would be necessary to denude the area for the beginning of development (see Wilson, '26).

8. LIFE SPAN AND RATE OF REPLACEMENT

Fraser and Smith ('28) found the age of the majority of Paphia was seven years, though a few were evidently ten years old. The same authors studied Saxidomus; the majority were about nine years old and a few sixteen years old. Approximately half of the clams breed at the end of the third year, the remainder in the fourth year. Such information is important as a basis for understanding community development, weather effects, etc. The other species of this community do not appear to have been studied. The life histories of the worms and gasteropods are quite unknown. Some Zostera-inhabiting snails of the Danish waters are annuals (Blegvad, '28).

9. PHYSIOLOGICAL CHARACTERS

Most of the experimental studies of important species from this community have been made on fishes. Among the fishes studied by the writer (1918) was the black spotted flounder (*Psettichthys melanostictus* Gir.), the remarkable resistance of which has already been noted in connection with the Pandora-Yoldia biome in which it occurs at times. As compared with Cymatogaster (Shelford, '18), it was three times as resistant to CO_2 and fifty times as resistant to H_2SO_3. This is in keeping with its habit of burying itself in the bottom. These experiments bring out the difference in physiological characters in accord with habitat and habits. This particular set indicates difference in the level occupied. In another group of experiments (Shelford and Powers, '15) the sole, *Lepidopsetta bilineata* (Ayres) was compared with *Oligocottus maculosus* Gir. Both were much more resistant to H_2S than the herring, but Oligocottus a little more resistant than the soles. The starry flounder, *Platichthys stellatus* (Pallas), takes on the color of the background after about 6 days, the results being fully as clear as in the flat fishes studied by Mast ('14). Cymatogaster responds to water conditions selecting water of pH 7.8 or 8.0 (Powers, '21). Andrews ('25) demonstrated that the young fishes of this species are much more sensitive to adverse conditions than the adults. All these facts have a bearing upon the abundance and habitat relations of the species.

10. SUCCESSION TO LAND

Where there are physiographic changes which lead to deposition or the enclosing of small arms of the sea, succession from the sea to land occurs. This is in fact the invasion of the sea area by the terrestrial climax of the region and is to be understood as of the same character as the tension between various other biomes. It is evident that this succession does not, in all cases, present the same or even similar stages between the Macoma-Paphia community and the first coniferous trees representing a terrestrial subclimax. Some of the strictly marine communities appear to indicate a trend toward land.

Haminoea, snail, and Epiactis, sea anemone, and Cymatogaster, the viviparous perch, are most abundant over muddy bottoms in protected bays and lagoons containing eel grass and not draining at low tide and appear to characterize this community. Most of the Macoma dominants are, however, present. The nearly enclosed tide-pool described by MacLean, page 319, probably represents a late stage following the Cymatogaster-Haminoea facies. (Macoma-Haminoea associes of Shelford and Towler, '25).

The suggestion that the Macoma-Upogebia facies (associes of 1925) is a forerunner of land stages appears less certain than at first. It is, however, certain that this tension line between sea and land communities prevents several intermediate types.

C. Strongylocentrotus-Argobuccinum Biome

1. Depth and Other Conditions

This biome occurs in 0 to 225 meters and is characterized by large echinoderms (Bush, '21), large snails, and pectens (Oldroyd, '24). A total list of possible dominants and influents would be a long one. Shelford and Towler ('25) listed only a small number of these that appeared to be of uniform occurrence and conspicuous in their characteristics. With the exception of a few that live under rocks, this community is characterized by animals that live on rather than in the bottom. Petersen would have characterized the Macoma-Paphia and Pandora-Yoldia biomes as characteristically "in-fauna," and the Strongylocentrotus-Argobuccinum biome as "on-fauna."

The submarine climate in this area is quite different from that of the Pandora-Yoldia area. The difference is most pronounced at the bottom. The salinity is higher, hydrogen ion concentration (Powers, '21) is higher, the plankton is less abundant, and, as was pointed out on page 267, the penetration of light is greater in summer, than in the Pandora-Yoldia area. It is doubtful, however, if light is an important limiting factor as regards the more important influents and dominants. Another important difference between the two communities is the presence in the Strongylocentrotus-Argobuccinum community of a much greater quantity and variety of large algae. Most of the red and brown algae require shells, or solid rock and stones for hold-fasts.

Probably the most important climatic factor is the circulation of the water due to tides. The community is composed of animals on the bottom and visiting the bottom. Much of the bottom is swept clean by rapid water movement. It is only in pockets that detritus has an opportunity to come to rest on the bottom and remain longer than the periods of minimal tidal fluctuations.

The work of Wismer and Swanson (Part II) has shown that the dominants and influents of this biome occur in the pockets and protected places, but are mixed with a very few of the Pandora-Yoldia dominants and a few related species of similar habits as, for example, a different species of Yoldia.

Some of these areas doubtless are permanent due to topographic conditions and represent faciations of the biome. Others, however, are subclimax areas which, with continued deposition will build up to a point where the retention of only coarse materials and shells will exclude species belonging to softer bottom, and hence, make the community quite typical of the average of the biome.

Three earlier studies of this community added to our general knowledge. Perry ('16) made an intensive study of a strip of bottom from high tide to 156 meters and showed the results in a table[8] indicating depth and abundance. The paper by Steggerda and Essex ('25) tended to show the widely distributed species.[9] H. Andrews ('25) made an important contribution in his study of kelp. Kirsop ('22) did the first bottom sampling and contributed important records.

2. BIOME PREVALENTS OR PREDOMINANTS

A. *Dominants and Slow-Moving Influents*

The figures indicate the number of individuals per 10 m_2. These are generally distributed throughout the biome.

Strongylocentrotus drobachiensis Mül., green sea urchin; 40-200.
Argobuccinum oregonensis Red., large snail; 2-50.
Balanus nubilis Dar., barnacle; 5-50.
Balanus pugetensis Pils., barnacle; 10-400.
Balanus rostratus Hoek, barnacle; 10-400.
Calliostoma costatum Martyn, snail; 2-60.
Psolus chitonoides H. L. Clark, sessile cucumber; 1-10.
Trichotropis cancellata Hinds, snail; 2-150.
Pecten hericius Gould, scallop; 15-1000.
Pododesmus macroschisma Desh., rock oyster; 2-50.
Amphissa columbiana Dall, snail; 5-85.
Orthasterias columbiana Verrill, starfish; 1-2.
Crepidula nivea C. B. Adams, slipper shell; 10-50.
Calyptraea fastigiata Gould, chinese hat; 3-6.

B. *Biome Prevalents Differing Markedly in Importance With Depth*

Strongylocentrotus franciscanus (A. Ag.), red sea urchin, locally important, 0-36m, but secondary, 36-125m; 4-60.

[8] In this paper for 'Balanus balanoides' read *Balanus cariosus*
'Balanus aquilla' read *Balanus nubilis.*
[9] In this paper for 'Islandis borealis Gil' read *Icelinus borealis* Gil.

Stichopus californicus Clark, large cucumber; few deeper than 35m; 5-30.
Modiolus modiolus Linn., deep water mussel; 10-3000.

c. *Biome Influents*

Icelinus borealis Gilb., northern sculpin; regularly present.
Myoxocephalus polyacanthocephalus (Pallas), giant sculpin.
Rhyamphocottus richardsoni (Gunther), gruntfish.
Hyas lyratus Dana, lyre crab; 2-10.
Cancer oregonensis Dana, small cancer crab; 1-20.
Oregonia gracilis Dana.
Pandalus danae Stimp.

d. *Characteristic Species Distributed Throughout but Few in Numbers.*

Styela stimpsoni Ritter, red tunicate.
Munida quadrispina Benedict, shrimp crab; wanting 1926-28.
Crago munita (Dana), shrimp.
Spirontocaris prionota (Stimp.), shrimp.
Hapalogaster mertensii Brandt, crab.
Pagurus kennerlyi (Stimp.), hermit crab.
Purpura foliata (Mart.), snail.

3. ASSOCIATIONS

In the earlier work (Shelford and Towler, '25) two associations were recognized, one from 0 to 35 or 50 meters and the other below this depth. Muenscher ('15) has discussed the algal communities as separate from the animals.

a. *Strongylocentrotus-Pugettia*[9a] *Association*

The biome prevalents (see page 281) occur mixed with those listed below.

(1) Dominants and slow moving influents of relatively uniform distribution: Figures are number per $10m^2$.
Cucumaria miniata Brandt, red cucumber; 2-20.
Cucumaria chronhjelmi Theel, cucumber; 2-30.
Crepidula adunca Sowerby, slippershell; 10-300.
Puncturella cucullata Gould, limpet; 3-6.
Petrolisthes eriomerus St., porcelain crab; very common near shore.

(2) Influents.
Ascelichthys rhodorus, J. & G., red-finned sculpin.
Aspicottus bison Gir., buffalo sculpin.
Sebastodes sp., rockfish.
Hexagrammos (Chiropsis) decagrammus (Pall.), 10-lined greenling; common.

[9a] This was called Strongylocentrotus-Cucumaria in 1925.

Blepsias cirrhosus (Pall.), silver spot cirrated sculpin.
Odontopyxis trispinosus Lock., pitted sea poacher; common.
Myoxocephalus polyacanthocephalus (Pall.), great sculpin.
Eumicrotremus orbis (Gunther), warty lump sucker.
Caularchus macandricus (Gir.), cling fish; common.
Pholis ornatus (Gir.), chameleon blenny; common.
Pholis lactus (Cope), chameleon blenny; common.
Bryostemma decoratum J. & S., decorated blenny.
Lophopanopeus bellus St. Roth., black clawed crab; abundant near shore.
Pugettia gracilis; graceful kelp-crab.
Epialtus productus (Ran.); decorator crab.

(3) Characteristic species.
Doriopsis fulva MacFarland, lemon-colored nudibranch.
Polypus hongkongensis Hoyle, devil fish; occasional.
Cryptochiton stelleri (Mittendorff), giant chiton.
Hinnites giganteus Gray, rockpecten.
Evasterias troschelii (Stimp.), starfish; regularly present.
Acmaea mitra Esch., tall limpet.
Ischnochiton interstinctus Gould, striped chiton.

(4) Faciations and Lociations of the Association.

The reader must understand that the figures given are meant to be estimates of the average over several hundred square meters; at maximum and minimum abundance. It must further be recognized that in years of minimum no representatives of several species will be found in some areas. Such of these variations as are large are called faciations. Faciations are usually associated with differences in bottom or water circulation while lociations depend upon minor features such as accidents of "seeding," early survival, etc. (Rice, page 293). The general character of her conclusions renders discussion of lociations useless.

a. Algal Faciations

One type of faciation dependent upon bottom, is described by Wismer and Swanson, p. 333. Others occur in reduced salinity. Perhaps the most important faciations are produced by the addition of the brown and red algae to the communities. These have commonly been treated as groups of dominants just as land plants are (Muenscher, '15), but the writer ('30) has pointed out the weakness and failure of this viewpoint in the Puget Sound in the following terms:

1. Algae are not present throughout the year and often constitute seasonal societies only.
2. They do not control the presence of the dominant animals but merely influence their numbers in some cases.

3. They are not uniformly distributed but occur only in small areas.
4. Very few or no influent and important animals are limited to them; those commonly found upon them are also on eel grass (Zostera). The influence of large plants is even less in the intertidal than in the subtidal areas.

Nereocystis-Laminaria (Melanophyceae)-Lacuna Faciation.

The brown algae constitute what has long been known as the "Laminarian Zone." The Algae were studied quantitatively by Gail (Shelford and Gail, '25) near Friday Harbor. The following species were taken, five or more plants per m^2: The faciation appears locally between 0 and 15 or 20 m, with all the biome and association predominants listed on page 282 present with the algae. The following are the more important algae. The figures following the name show depth limits in meters.

Nereocystis luetkeana (Mert.) Post. and Rupr., 1-15; *Laminaria* sp., 1-20; *Alaria* sp., 1-20; *Agarum fimbriatum* Harv., 5-20; *Desmerestia media* (Ag.) Grw., 1-15; *Desmerestia ligulata* (Lightfoot) Lamour, 5-30; *Costaria costata* (Turn.) Saunders, 1-20.

Animal species associated with the kelp (Nereocystis):

Lacuna porrecta Carp., snail.
Lacuna divaricata Fabr., snail.
Caprella sp. amphipod.
Pentidotea resecata (Stimp.) isopod.
Margarites succinctus Carp., snail.
Epiactis prolifera Verrill, sea anemone.

The animals of the holdfasts of Nereocystis were studied by Andrews ('25). Practically all of the species found by him were regular inhabitants of the other parts of the habitat of the Strongylocentrotus-Pugettia Assotion.

Dasyopsis-Halosaccion (Rhodophyceae) Faciation.

The red algae are distributed in patches and are most important in the lower half of the depth belt occupied by the Strongylocentrotus-Pugettia Association. There is a relatively wide area in which the brown and red algae are mixed. The animals seem not to show a difference corresponding to the different kinds of algae, but all the wide ranging biome prevalents as well as those characteristic of the association occur. Certain mud-bottomed areas well supplied with shells frequently show large masses of algae. Occasionally crabs, shrimp and blennies show a deep red color corresponding to that of the algae, which color is not characteristic of other individuals of the same species occurring elsewhere (Gamble, '10).

The algae (Rhodophyceae) of this faciation as studied by Gail (Shelford & Gail, '22) are the following. Figures indicate depth limits in meters.

Dasyopsis plumosa (Harvey & Bailey) Schmitz, 5-30; *Halosaccion glandiforme* (Gmelin) Ruprecht, 10-30; *Callophyllis* sp. (possibly *furcata* Farlow, 5-25; *Nitophyllum latissimum* (Harv.), J. Agardh, 15-25; *Agardhiella tenera* (J. Ag.) Schmitz, 5-35; *Rhodymenia pertusa* (P & R) J. Ag., 5-25; *Callymenia phyllophora* J. Ag., 15-30; *Iridaea laminarioides* Bory, 5-25; *Odonthalia semicostata* (Mertens) J. Ag., 10-25.

b. Other Faciations

Cardium-Yoldia Faciation.

The mud bottom faciation described by Wismer and Swanson (page 333) is characterized by the presence of *Cardium californiense* Desh. and *Yoldia scissurata* which is an indication of mud bottom. These occur in addition to the prevalents listed on page 281.

In the following list of associated species the figures indicate the number of individuals in $10m^2$, see data by Wismer and Swanson, p. 340.

Yoldia scissurata Dall., 10-900.
Cardium californiense Desh., 10-80.
Solen sicarius Gld., 10-30.
Nucula castrensis Hinds, 2-400.
Polinices pallida B. & S., 300-600.
Venericardia ventricosa Gld., 1-100.
Marcia subdiaphana Carp., 10-80.
Crago alaskensis Lock.

With the exception of the *Marcia subdiaphana* the species listed are in part characteristic of the ecotone between the Pandora-Yoldia Strongylocentrotus-Argobuccinum biomes as described on page 270. *Marcia subdiaphana* is an important prevalent in the Pandora-Yoldia community. *Yoldia ensifera* which is important in portions of that community, was represented by a sparse population (see pp. 269 and 344).

Pisaster Ochraceus Faciation.

Pisaster ochraceus (Brandt) is an ecotone species occurring in the very upper edge of the Strongylocentrotus-Pugettia community and in the tidal community. It is not sufficiently abundant to have any marked influence, except above the Pandora-Yoldia areas. Here there is an unusual arrangement of communities which is very important from the standpoint of the presence of various species (Fig. 4). The Pandora-Yoldia areas are characterized by mud bottom and little wave action at a depth of two or three meters, below low tide. They commonly give way to a marginal strip of poorly developed Strongylocentrotus-Pugettia community containing *Pisaster ochraceus* (Brandt) and green sea urchins. Large cucumbers, *Stichopus californicus* Stimp., and especially *Cucumaria miniata* (Brandt) in abundance, characterize this area.

This arrangement of the animals and conditions which they indicate, explains the occasional presence of stray motile species of the Strongylocentrotus community on typical Pandora bottom. An occasional *Stichopus californicus* is found on the Pandora bottoms, but is interestingly dull in color and sickly in appearance. This arrangement of communities shown in Figs. 4 and 7 is particularly important in connection with occurrence of fishes, crabs, etc. Species of fishes and crabs belonging properly to the Strongylocentrotus community are found occasionally in the shallower parts of the Pandora-Yoldia community adjacent (see pages 262 and 314).

B. *Strongylocentrotus-Pteraster Tesselatus Association*

This is mainly below 36 to 50 meters, down probably to 225 m. Since 1925 the community has been examined in the deeper waters especially down to 225 meters, south of Flat Top Island. In the deep water at and above 225 meters the wide ranging dominants remain as elsewhere except at this point and south of Turn Island where *Chrysodomus liratus* Mart., the large snail, takes the place of *Argobuccinum*.

(1) Dominants and slow-moving Influents.

(See also those listed on page 281). Figures indicate the number of individuals per $10m^2$.

Crossaster papposus (L.) M. & T., rose star; 3-6.
Pteraster tesselatus Ives, cushion star; 2-4.
Gorgonocephalus eucnemis M. & T., basket star; 1-3.
Terebratulina unguicula Carp., brachiopod; 10-30.
Hemithyris psittacea Gmel., brachiopod; 10-20.
Evasterias acanthostoma Verrill, star fish.
Ptilosarcus quadrangularis Moroff, sea pen; 2-4.
Aglaophenia struthionides (Murray), ostrich plume hydroid.
Pecten hindsii Carp., scallop; 5-100.
Modiolus modiolus Linn., deep water mussel.

Pectens and barnacles are more abundant and *Stichopus californicus* is usually less abundant, than in the shallower water association.

(2) Influents.

Gilbertidia sigolutes (J. & S.), Gilbert's sculpin; common.
Microstomus pacificus (Lock), smeardab.
Nautichthys oculo-fasciatus Girard, sailor fish.
Asterotheca alascana (Gilbert), rat-tail fish; Alaskan seapoacher.
Pandalus stenolepis Rath, shrimp.
Pandalus borealis Kröyer, pink shrimp; common.
Pandalus montagui tridens Rath., Montague's shrimp.
Pandalus jordani Rath., Jordan's shrimp.
Chorilia longipes Dana, crab; 2-10.

The biome dominants and influents extend throughout, mixed with the association influents and dominants. The climate is characterized by lower temperature, less light, more constant conditions, and less plankton and floating detritus, than that of the Strongylocentrotus-Pugettia association.

(3) Faciations.

Faciations occur in this association due to differences in circulation, bottom materials, etc.

a. Modiolus Faciation

Under certain submarine climatic conditions, chiefly below 35 m and down to 225 m and below, *Modiolus modiolus* (Linn.) occurs as an important dominant in the Strongylocentrotus-Argobuccinum biome. A similar community is important in the North Atlantic (Sparcks, '29). In San Juan Channel there are areas in which this species occurs covering mud or clay bottoms, usually in depressions protected from tidal currents. These appear to be areas in which Modiolus is a true dominant and the community is at least two-layered, sometimes possibly three-layered. The probable layers are composed of animals (1) *on* the Modiolus, (2) *among* the Modiolus and (3) in the mud *below* them. Worms live below the Modiolus.

Modiolus appears to occur in solid masses of 2,000 or more on ten square meters. The beds do not appear to be continuous and estimates of 3,000 to 4,000 per 10m^2 are about the maximum. They do not occur on all muddy bottoms and become very scattered at and above 35 meters depth (Wismer and Swanson, page 340.

All the principal dominants and more important influents belonging to the entire biome and those restricted to the Strongylocentrotus-Pteraster association occur through the area controlled by Modiolus. Modiolus supplies the substratum necessary for their attachment and they are often quite abundant. It is not clear from the investigation what lociations occur or the difference between this and the climax on mud below dead shells. A number of worms have unfortunately not been identified. Some of these, scaly worms (Polynoidae) and the sea mouse (Aphroditidae), which are perhaps characteristic, and Nereidae, are present.

4. EXTENT AND RANK

This community occurs on the west coast of Oregon, Washington, and Vancouver Island and evidently covers much bottom quite continuously. Its general range is unknown but its occurrence on the west coast of Vancouver Island in Barkley Sound was indicated by shore examination and a small amount of dredging with a small naturalist's dredge operated by hand in 1930. This locality is on the open shore of the Pacific. The water is subject to considerable dilution by the heavy rain of the coast especially in winter. The wave action is that of the open ocean coast. The following species were well represented:

Strongylocentrotus drobachiensis O. F. Mul., green sea urchin.
Strongylocentrotus franciscanus A. Ag., red sea urchin.
Balanus nubilis Dar., large barnacle.
Pugettia gracilis Dana, graceful kelp-crab.
Ischnochiton radians Carp., chiton.
Ischnochiton mertensii Midd., red chiton.
Lepidochitona ruber Linn., chiton.
Amphissa columbiana Dall., snail.
Margarites pupillus Gould, snail.
Calliostoma canaliculatum (Martyn), snail.
Crepidula orbiculata Dall., slipper shell.

There are, doubtless, associations covering a part of the range, as well as those recognized as dependent upon depth. In its contact with the Pandora-Yoldia biome, the boundary is sharp and the ecotones narrow. The boundary between this community and the Macoma community is wide in proportion to the width of the latter, being equal to one half or more of the width of the Macoma-Paphia biome.

5. INTERACTION IN THE BIOME

The great variety of large organisms which make up the dominants and influents of this community make possible many inferences as to interaction from the general habits of these species.

A. *Coaction*

One of the most important coactions was studied by Weese ('26) who worked on the food of an important dominant, the green sea urchin. Its food included more than fifty per cent plant material, chiefly fragments of plants growing in shallow water. Animal food included Balanus, Bryozoa, sponges, and hydroids.

The considerable number of sea urchins present and the action of these in scraping the smaller plants and animals from the substratum is important (Weese, '26). The various starfishes play an important rôle. Though present in small numbers, their large size renders them potent attackers of barnacles, which are present in some abundance also. They also feed upon other forms. Argobuccinum, Calliostoma, Amphissa, and other snails probably prey upon the sedentary species. Very little is known of the food of the crabs and fishes. Snails supply shells for hermit crabs, etc.

B. *Reactions and Succession*

The surface of nearly all rock is encrusted with bryozoans, shells of barnacles, rock pectens, serpulids, etc., and, in the shallower water, the bodies and hold-fasts of algae. The loose skeletons of molluscs, barnacles, and

echinoderms form beds of considerable extent in pockets swept by currents. In many places with bottom of fine materials, the shells of mollusca form important places of attachment for barnacles, chitons, and algae. The detritus from algae and Zostera, etc., is important as food for animals and as a part of the floating materials influencing the marine climate.

Mud and sand lie in depressions in the bottom. Such physiographic inequalities are gradually eliminated by current action which fills the depressions. When nearly filled shells and other coarse materials are deposited and mud bottoms become covered with shells. The mud bottom faciation is succeeded by the typical composition of the association.

6. PHYSIOLOGICAL CHARACTERS

A long series of experiments by the writer ('16)[10] was concerned with resistance to temperature and fresh water. The shrimps which occurred in great abundance were above 30m and were two or three times as resistant to freshwater at a temperature of 24°C. as shrimps below 30m. The 30m line roughly marks the division between two associations. However, scattered individuals of shallower water shrimps found in deep water were also less resistant but at the same time more resistant than the species largely confined to the deeper water. The same general principle holds good for the crabs and echinoderms.

The series of experiments brought out radical differences between the Balanus-Littorina and Strongylocentrotus-Argobuccinum biomes through the comparison of similar species of barnacles, mussels, etc.

D. BALANUS-LITTORINA BIOME

This community is associated with the Macoma-Paphia biome and there has been some confusion. The relative levels at which these two biomes occur must be clearly in mind. In those parts of the area of study where the tidal range in level (as indicated by animals) amounts to about 3m, a hard substratum is completely occupied by the Balanus-Littorina biome. The Macoma-Paphia biome, however, rarely reaches above 1½m below the higher tides, or, in other words, overlaps about half the belt of the Balanus-Littorina biome. The Macoma biome extends downward at least 8m below the lower limit of the Balanus-Littorina biome. Where there is a suitable upper shore substratum the Balanus-Littorina biome is to be expected above the Macoma-Paphia biome. Rocks imbedded in tidal Macoma sands are commonly covered with tidal Balanus and associated forms. In other cases where there is not much deposit of sand, the higher portions of a beach are often gravel and are covered with Balanus and Mytilus. Occasionally the two may overlap with the Macoma beneath ("in-fauna") and the Balanus above ("on-

[10] In this paper for "*Balanus balanoides*" read *Balanus cariosus* (Pallas) and for "*Balanus aquilla*" read *Balanus nubilis* Dar.; transpose "All alive" and "All dead" after first two species in Table 5, p. 167.

fauna"). Thus the two intermingle like grassland and forest to make a park land savanna.

The presence of Balanus-Littorina species on fine gravel or sand is, as much or more a matter of general hydrographic conditions as of substratum. Even fine sand beaches in protected bays frequently have their higher reaches partially covered with *Mytilus edulis* which forms a substratum to which *Balanus glandula* is attached.

This community is strictly tidal on the north Pacific shores examined. It is normally exposed throughout its extent at medium low tide and it, together with a considerable area of the community below, is exposed at the extreme low tide. Peculiarities of the arrangement of the species within this biome throw much light on the general question about communities. It has been more thoroughly studied than any of the major communities of the waters under consideration. The work done by Shelford and Towler ('25) included a reconnaissance of the shore over a considerable distance shown in their maps (pp. 48-50). At the outset they recognized several degrees of community luxuriance, one or two in addition to those indicated on the map on page 53, but part of these had to be dropped. This was due to the fact that in making the reconnaissance over 132 km (80 miles) of mainly broken coast, it was not possible to identify barnacles beyond the point of determining that the *Balanus cariosus* was almost universally present on stationary objects. Since that time, studies of barnacles by Towler ('30), Worley ('30), and Rice ('30) have shown that in enclosed bays, inner ends of coves, etc., *Balanus glandula* Dar. increased and *Balanus cariosus* (Pal.) decreased, especially in the upper portion of the community. On the whole Worley found *Balanus cariosus* was more abundant in waters of lower salinity, and larger in waters of higher salinity. Rice concluded that low salinity favored a great abundance of barnacles on reefs offshore, the greatest abundance being in 26-28 gm. per 1. The relations as observable at any time are likely to be contradictory because of their determination by a series of events at the time of seeding.

1. ASSOCIATIONS AND FACIATIONS

Shelford and Towler not only evaluated the grades of the Balanus-edulis association which we call *faciations* in this paper, but two associations were recognized. In 1929 after a trip to Alaska and Southern California in which barnacles were collected, an attempt was made to clarify these two associations. The writer was not able to identify all the barnacles in place and from the collections made, *Balanus hesperius* Pils. was given a place not justified by the observations at La Jolla by Rasmussen. Rasmussen found that three of the principal species are different at La Jolla and in the Pugent Sound region. In Southern California *B. cariosus* is not numerous and never dominant. It has no equivalent except possibly *Tetraclita squamosa rubescens* Dar. The

place of *Chthamalus dalli* is taken by *C. fissus* Dar. and that of *Littorina sitchana* and *L. scutulata* by *L. planaxis* Phil. The suggestion of a Mitella-Mytilus association in 1930 has not been justified by subsequent observations. An unusually definite and significant arrangement of the dominants was found at Barkley Sound (station 23 and 24).

A. *Balanus-Mytilus californianus Association*

In Barkley Sound (west coast of Vancouver Island) the arrangement of the predominants of the Balanus-M. californianus association on one of the Chain Islands (Holy Island) was very illuminating. Here on the outside of the island facing the open Pacific the principal dominants of the community as a whole are arranged in very definite faciations on slopes and vertical cliffs. These are four in number, arranged as shown in the Table 4. The principal dominant in each faciation is named first.

TABLE 4. LIST SHOWING THE FACIATIONS OF THE BALANUS-M. CALIFORNIANUS ASSOCIATION IN BARKLEY SOUND

Opposite the name of the species is the average per m².
Balanus-californianus Association, 190 cm. wide.

1. Littorina-glandula Faciation, 20 cm wide.	
Balanus glandula Dar., barnacle	2400
Littorina scutulata Gould, snail	200
2. Littorina-cariosus Faciation, 45 cm wide.	
Balanus cariosus (Pallas), barnacle	3140
Littorina scutulata Gld., snail	228
Acmaea digitalis umbonata (Nutt.), roe limpet	70
Thais emarginata Desh., snail or whelk	38
3. Mitella-Mytilus Faciation, 65 cm wide.	
Mytilus californianus Conrad, California mussel	1943
Mitella polymerus (Sow.), goose neck barnacle	1506
Balanus cariosus (Pallas), barnacle	1363
Red sea anemone	120
Littorina scutulata Gld., snail	225
Littorina sitchana Phil., snail	50
Thais emarginata Desh., snail or whelk	180
Acmaea digitalis umbonata (Reeve), limpet	110
Acmaea cassis Esch., limpet	380
4. Cribrina Faciation, 60 cm. wide.	
Cribrina xanthogrammica (Brandt), green sea anemone	3140
Balanus cariosus (Pall.)	4
Chitons	40
Pisaster ochraceus (Brandt), common starfish, an ecotone species	6
Mytilus californianus Con., Calif. mussel	20
Chthamalus dalli Pils.,[11] small barnacles	3000

In the Mitella-Mytilus Faciation area, *Mytilus californianus* is a true dominant, as it covers rock surface and quite completely excludes *Balanus cariosus*. Individuals of this species were small and seated on the shells of the *Mytilus californianus*. The arrangement appears to be similar to that observed by the writer at Taft, Oregon (Shelford, '30). It appears that this arrangement may be quite common on the wave-swept headlands of a con-

[11] Chthamalus does not average this density over the area but occurs in local clans having about this number per m².

siderable part of the coast of Vancouver Island, Washington, Oregon, and perhaps northern California.

B. *Balanus-Mytilis edulis Association*

Fifteen meters from the point described in Table 4, around the north side of Chain Island, *Mytilus californianus* gives way to *Mytilus edulis* Linn., first at the top and finally throughout its zone. The definite arrangement of the species making up the communities disappears and they become quite generally mixed together. On the inside of the island all definiteness of arrangement disappears. The inside is exposed less to wave action and more to fresh water while the outside is definitely exposed to the surf and waves. The writer recognizes only the two associations originally described by Shelford and Towler ('25).

A few miles west of Port Angeles, Washington, all the principal species of the biome appeared on the same shore and were quite generally mixed together. This is on the south shore of the Strait of Juan de Fuca and in the transition between the communities which may contain Mitella and *Mytilus californianus* as important general dominants and those in which the former occurs in clans and the latter is not abundant. Likewise Clements (personal communication) finds that all the principal dominants of the deciduous forest occur together in certain parts of Kentucky, though in other places they are separated into three associations: oak-hickory, beech-maple, and oak-chestnut, each with a rather large distribution area. Some of these are separated into consociations as for example: a *beech consociation*.

2. LOCIATIONS

A. *Tide Pools*

Tide pools have received much attention on account of the ease with which they may be studied. Tide-pools which lie within the intertidal community level are usually lociations of the tidal community (Gersbacher and Denison, '30) except where the bottom is sand. Sand-bottomed pools with rock walls are not common. The usual rock-bottomed tide-pool contains both common species of Balanus, the two species of Littorina, also Mytilus, limpets, hermit crabs and snails which frequent the tidal area and are regularly found out of water at low tide. In addition, fishes which stay near the water margin and hence are quasi-residents of the biome. To these are added a few sub-tidal animals such as a Cucumaria, serpulids, and occasional snails and chitons.

B. *On Rock Faces*

Variations in the arrangement of dominants and influents on relatively similar shores are due to mere local conditions and the effect of weather, tide, etc., during the early part of the individual life-history.

DYNAMICS AND EXTENT OF BOTTOM AND SHORE COMMUNITIES

By

LUCILE RICE, D. I. RASMUSSEN, V. E. SHELFORD, A. O. WEESE, ARCHIE MACLEAN AND H. C. MARKUS

I. BALANUS-LITTORINA BIOME

A. FACTORS CONTROLLING ARRANGEMENT OF BARNACLE SPECIES IN TIDAL COMMUNITIES

LUCILE RICE

Several papers have been written in regard to the distribution of tidal barnacles in the Puget Sound region. Shelford ('30) and Towler ('30) indicate that they group themselves into definite communities, and Worley ('30) and Rice ('30) indicate that low salinity favors abundance, seeding and the survival of young barnacles.

Very little is known about the rate of seeding, conditions controlling the survival and the time of most abundant seeding. Pierron and Huang ('26) whose observations covered the period from June 20 to August 2 only, state that the greatest attachment upon denuded rocks just off Brown Island occurred early in July, and that a few died after each period of attachment. Johnson (unpublished) shows that March, April, May, August, September, October 1929-30 were the months of most abundant survival of young barnacles on rocks and pilings under the pier at Friday Harbor. These authors did not determine the species.

The purpose of this study was (1) to check the abundance of mature barnacles at some of the stations observed in 1928 (stations 1-15) (Rice, '30); (2) to check on the survival and abundance of young of the different species (June 17 to August 18, 1930); and (3) to throw further light on the effects of pollution, weather, type of bottom, tide, and salinity upon the survival of young barnacles. To accomplish this stations 16 to 22 were added.

The species considered are *Balanus cariosus* Pal., *Balanus glandula* Dar., *Chthamalus dalli* Pils., all of which are tidal.

Actual counts of young barnacles per dm^2 were made at the first (top), second (middle), and third (bottom) meter levels of the tidal area and when possible the species were identified.

1. FLUCTUATIONS IN NUMBER OF YOUNG BARNACLES WITHIN SHORT PERIODS

Fifteen stations were established. The more important were observed at approximately ten day intervals, others less frequently. Some of the stations located on the salinity map of Shelford ('30) were used again.

A. *High salinity and rough water station*

(1) Seeding and survival on undisturbed rocks.

This station (station 12) was in an area of the highest salinity (30 gm per 1) with continuously rough water available. It was located on a rocky point at Kanaka Bay and got the full force of the waves and incoming tides from the ocean through the Juan de Fuca Strait. The rocks were either abrupt or gradually sloping and exposed to the sun when not covered by the tide.

Along with the plots mentioned an area of barnacles 1 dm^2 was carefully outlined with white paint and all barnacles plotted and counted. All dead were picked off each time. From these areas estimations were made for Fig. 5.

It was noticeable in these marked areas that with the exception of *C. dalli,* the young which attached to the old barnacles had a much better survival than those which attached to the bare rock.

The older barnacles, ranging in diameter from 10 mm to 40 mm held constant throughout the period and were distributed in levels as follows: 1st meter below average high tide *B. cariosus* 1000 per m^2; 2nd meter *B. cariosus* 8000 per m^2; 3rd meter *B. cariosus* 2500 to 3000 per m^2; a few *C. dalli* scattered through the second and upper half of the third meter; no *B. glandula* at any level.

Fig. 5 shows the total population at station 12, rate of attachment, survival and death rate by species of the young barnacles for six observations made from June 21 to August 11, 1930.

The young barnacles at all three meter levels for the first observation, June 21, were *B. cariosus* from 1 to 5 mm in diameter; most of them were 5 mm or more showing that they were several weeks old.

The second observation showed a heavy attachment of all three species. Most of the *B. cariosus,* observed during the first period, were living and had increased in size approximately 1 mm.

The third observation showed a high death rate and a few attachments by both *B. cariosus* and *B. glandula* in the first and second meter levels, and an increase in the third meter. *C. dalli* increased greatly in the first and second meters.

The fourth observation showed many dead *C. dalli* followed by great increase during the period to the fifth and sixth observations. Every available space was densely set with them. They do not very often attach to other barnacles. *B. cariosus* held fairly constant during the third period (fourth observation) and increased during the fourth and fifth periods. All of the *B. glandula* in the third meter died, increased again at all three levels during the fourth period, to die again at the second and third meter levels during the fifth period.

The following percentages of the three species of young barnacles present June 21 were living August 11; first meter *B. cariosus* 3%, *B. glandula,* 0%, *C. dalli* 0%; second meter *B. cariosus* 10%, *B. glandula* 5%, *C. dalli* 0%; third meter *B. cariosus* 15%, *B. glandula* 0%, *C. dalli* 0%.

This percentage of survival of young barnacles compares rather favorably with the number of mature barnacles found at the same levels. From a study of the small percentage of survival of young as seen by Fig. 5 and from others observations made on nearby areas it is made evident that barnacles attached to unprotected surfaces after the first or middle of June had little chance of survival during the warmer weeks of July and August.

Barnacles more than 10 mm in diameter at the first observation (June 21) were not enumerated in the counts used in the graphs. These older barnacles changed very little in abundance but increased in size from 10 mm to 15 mm during the seven weeks.

(2) Seeding and survival on denuded and planted rocks.

At the first observation, June 21, an area of 1 m^2 was cleared at all three levels by removing both the old and the young barnacles. In addition to this, rocks from land were placed out at one, two and three meters below high tide. The young barnacles did not survive on these planted rocks suggesting that the effects of other organisms may be essential. They attached and grew as large as 0.5 mm to 1 mm in diameter but were dead at the next observation, with the exception of a few which attached to the under side of one of the rocks. On the cleared area at the third meter level one sixth of the new sets of *B. cariosus* survived at the end of each period and were not included in the graphs.

B. *High salinity—Quiet water Station*

Fig. 6 (station 8, located on the east side of Brown Island) shows the fluctuation of young barnacles in a well protected area. The salinity here is 29 gm per 1 and there is very little wave action. This figure compares very favorably with Fig. 5 for survival and death rate except for the last two periods. During the week prior to July 28, a great amount of oil ran into the bay and apparently killed all of the young barnacles. At any rate all of the barnacles on July 28 were very young measuring 0.5 to 1 mm in diameter; and many of these did not survive the hot weather and low tides from July 28 to August 8.

Areas which had a heavy covering of Ulva examined on August 8 showed a heavy stand of young barnacles measuring in diameter from 2 to 10 mm. These were well protected from sun, and the oil which collected on the plants, did not get through to the rocks below.

(1) Effect of tides and weather.

When Figures 5 and 6 are compared the periods of most abundant seed-

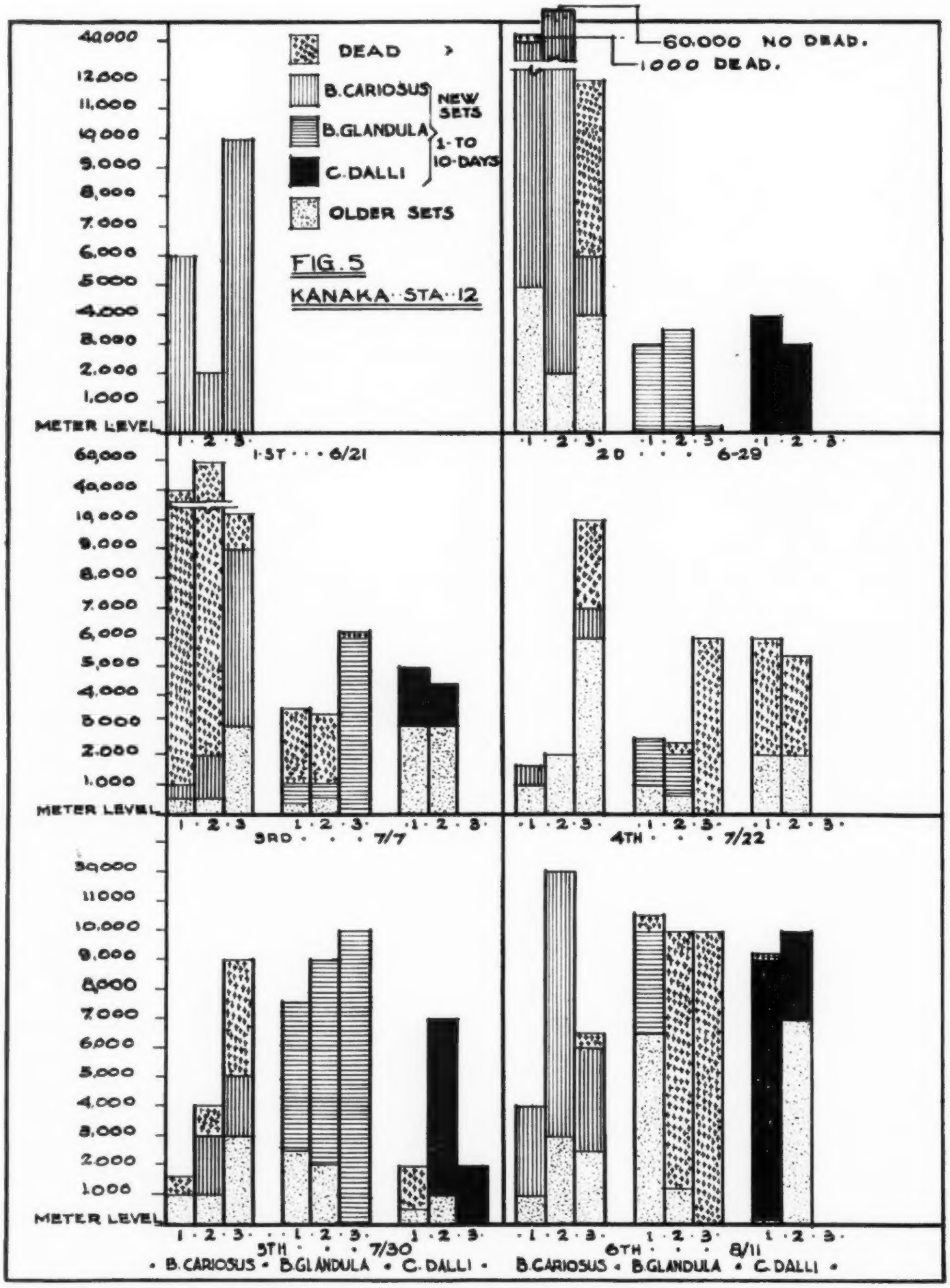

FIG. 5. Showing the total population, rate of survival, attachment and death of young barnacles per m² over three vertical meters of shore which are covered and uncovered with the average change of tide. High tide is zero. The horizontal scale is in meters below high tide, the vertical scale is in numbers of individuals per square meter. Data are for six periods of approximately ten days each, from June 21 to August 11 at Kanaka Bay (station 12), rough water, high salinity (30 gm per 1).

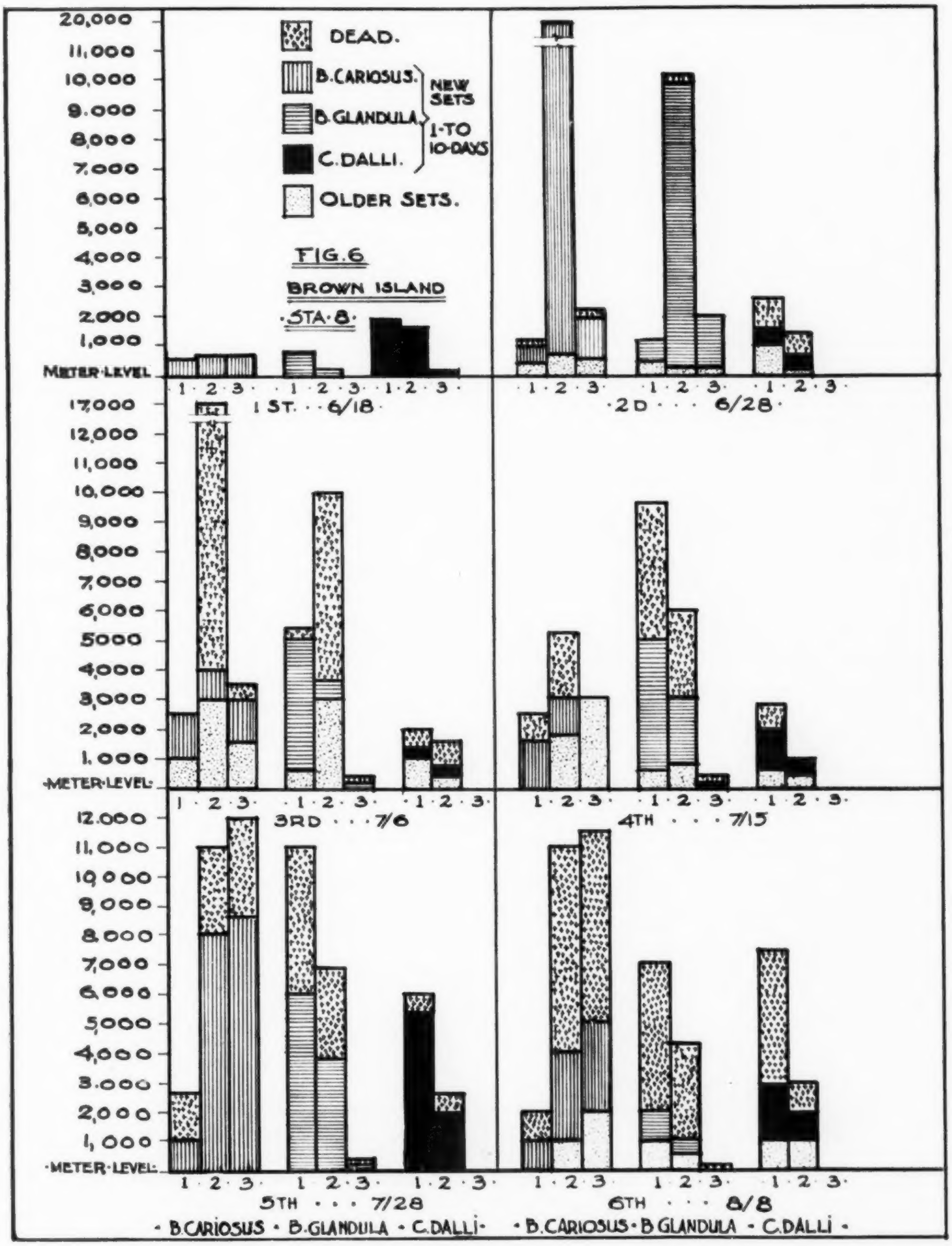

FIG. 6. Similar to Fig. 5 with same legend. Data for six periods of approximately ten days each, June 18 to August 8. Brown Island (station 8) quiet water, high salinity (29 gm per 1). Lack of survivals of all species at the fifth observation is probably due to a large amount of oil poured into the harbor during this period.

ing for a given area are found to run in cycles. Seeding and survival of the different species fluctuate considerably at different levels.

From a study of these two, Figures 5 and 6, and Table 5 which shows the tide and weather conditions for the whole period, it is apparent that the

heaviest seeding of the whole period took place between June 21 and June 29, through a period of the highest, and lowest of the low tides. However, the lowest tides occurred between 8 and 12 A.M. and the weather was cool and cloudy. (See U. S. Dept. of Com. Tide Tables for 1930.)

The highest death rate and poorest seeding were between June 29 and July 22. During this period the weather ranged from moderate to very hot and dry and all of the low tides came between 7:50 A.M. and 1:30 P.M. The best survival of young at this time took place in the protected crevices and at the third (lowest) meter level.

From July 22 to August 11 there was an increase in the amount of new attachments and in the survival of the old. Though the weather was dry and hot the fact that the lowest tides came between 7:00 and 11:30 A.M. and did not fall as low, apparently protected the barnacles.

Observations made at stations 12 and 8 on July 28 in plots other than those used for the graphs showed on all surfaces exposed to the sun, conditions similar to those shown in the graphs for that date. In crevices under Ulva, and on the shaded side of rocks in the second meter, numbers were estimated as 20,000 *B. cariosus* and 10,000 *B. glandula* per m^2 ranging in size from 1 to 15 mm. Approximately two-thirds of each were from 10 to 15 mm in diameter; the other third was 1 to 3 mm. The third (lowest) meter showed 4000 to 5000 *B. cariosus,* 1 to 15 mm, and 12 to 14 *B. glandula* 1 to 10 mm, the ratio of sizes about the same as for the center meter. Station 8 showed similar survival. The number of attachments was never at any time as great at this station as at station 12.

TABLE 5. Tides and weather condition, 1930. Heights in feet.

Date	Height of Low tide	Time	Prevailing weather
June 16–22	-0.1 to 0.5	2:00 P.M. to 6:56 A.M.	cool, cloudy
June 23– 1	-0.7 to 0.0	7:31 A.M. to 1:33 P.M.	cool, clear to cloudy
July 2– 6	1.6 to -0.3	2:23 P.M. to 7:15 A.M.	moderate
July 7–14	-0.8 to -0.3	7:50 A.M. to 11:57 A.M.	cool first part, hot last part
July 15–20	0.5 to 1.0	12:33 A.M. to 5:30 A.M.	moderate
July 21–29	-0.1 to 0.1	6:13 A.M. to 12:21 P.M.	hot, dry, bright
July 30– 3	1.6 to 0.3	1:05 P.M. to 5:54 A.M.	hot, dry, bright
August 4– 9	-0.2 to -0.5	6:42 A.M. to 9:50 A.M.	hot, dry, bright
August 11–15	0.2 to 3.9	10:54 A.M. to 1:10 P.M.	cooler

c. *Comparison of High and Low Salinity Stations*

(1) A muddy bay in a high salinity region and a muddy bay in a low salinity region.

On the northwest end of San Juan Island there is a long shallow bay known as Wescott Creek. It is two miles long and one mile wide, and has mud bottom throughout except at the entrance and ranges in depth from 1 to 10m, see (MacLean, p. 319).

The water is quite muddy most of the time, especially during tide movements but there is little wave action except during storms. Great quantities of dust from the lime pits nearby cover the water and form thick crusts over all the barnacles.

Winter conditions in this bay are not known but there is a possibility that much fresh water may come in at this time from streams at the head of the bay. During the summer there is no fresh water entering and the salinity ranges from 29 to 30 gm per liter.

Every available stick, stone and rock was covered with very large *B. glandula* and *B. cariosus* through all three levels.

First (top) meter: *B. glandula*, 1500-2000 per m^2, 20mm in diameter.

Second meter: *B. glandula*, 1000-1500 per m^2, all attached to *B. cariosus*. *B. cariosus*, 100 to 120 per m^2, 20 to 60 mm in diameter, 20 to 70 mm tall.

Third meter: *B. glandula*, 300 to 400 per m^2, 15 to 20 mm in diameter, covered the *B. cariosus*. *B. cariosus*, 50 to 100 per m^2, 40 to 70 mm in diameter, 20 to 70 mm tall. Almost all were old and heavily encrusted with mud. The young were very few.

In a small mud bay at Point Roberts at the mouth of the Frasier River barnacles of all species were more abundant than at any place previously observed.

The salinity of this station was not determined but it is nearer the Fraser River than the Sucia Islands about which the salinity was 26 gm. per liter.

On account of the splitting of the river by Lulu and Westham Islands fresh water carrying much sediment flows toward the Point, and into Boundary Bay, and forms large mud flats. Three miles of shallow beach may be exposed at low tide. Wave action is severe on exposed points and seems to prevent attachment except in protected spots. Here again every available stick, stone and rock was densely populated with barnacles. They were very long and slender, 2 to 4 mm in diameter and 15 mm high. The first (top) meter showed 202,800 *B. glandula* per m^2 growing very close together and piled on one another. The greatest abundance was on the shaded side of the rocks.

In the second meter level there were 2280 *B. cariosus* per m^2 10 to 15 mm in diameter and 27 mm tall; these were covered with small *B. glandula* 3 mm in diameter and 2 mm high, 4000 per m^2. The third meter level had the same *B. cariosus* count and very few *B. glandula*.

C. dalli was more abundant, extending higher and lower than any of the other barnacles. Every spot not occupied by other barnacles was piled high with these barnacles. 42,400 *C. dalli* per m^2 were counted above the *B. glandula* line and 236,600 *C. dalli* per m^2 were counted below the third meter level (see Huntsman '18).

Table 6 shows that the bay at Point Roberts in an area of low salinity is

favorable for successful attachment and survival, and consequent small size of barnacles; while the bay at Wescott Creek is characterized by smaller numbers but successful individuals attain large size.

TABLE 6. Comparison of barnacles in an open mud bay with low salinity and a closed mud bay with high salinity.

Species	Meter level	Station 22—Point Roberts Low Salinity			Station 17—Wescott Bay High Salinity		
		Number per m^2	Size, mm		Number per m^2	Size, mm	
			Diameter	Height		Diameter	Height
B. glandula...	1	202,800	2-4	15	2,000	20	30
B. cariosus...	1	0	0	0	0	0	0
B. glandula...	2	4,000	3	2	1,500	20	30
B. cariosus...	2	2,280	10-15	27	120	20-60	20-70
B. glandula...	3	500	3	2	400	30	40
B. cariosus...	3	2,280	10-15	27	100	40-7	20-70

C. dalli was scarcely noticeable at Wescott Creek but was extremely abundant at Point Roberts. It seemed that 1930 was a favorable year almost everywhere for this barnacle. It was so inconspicuous in 1928 that it was seldom considered.

Nothing is known about the environmental conditions in these bays. Gran and Thompson ('30) in a study of diatoms within the San Juan Archipelago mention that the freshwater coming in from the Fraser River is extremely favorable for the growth of diatoms.

The extreme size and abundance of *B. glandula* is noticeable at Wescott Bay while the small size and extreme abundance of both species is evident at the other station.

2. CHANGE IN COMMUNITIES IN A TWO-YEAR INTERVAL (salinity 26.5-28-0 gm per 1)

Many of the stations (salinity 26.5-28.0 gm per 1) visited in 1928 and described in the author's paper ('30) showed changes in 1930. (For station locations see Fig. 1, also map, Shelford, '30, p. 223. Station 19 unnumbered.)

A. *Blind Bay near Orcas—Station 19*

Blind Bay on the northeast side of Shaw Island has two types of shore line, long gradual sloping gravel beach on the east side and a vertical rocky cliff on the west. In 1928, all available rocks and loose gravel on the gradually sloping east shore were covered with dense masses of mature *B. glandula* through the first, second and third meter levels. The rugged rocks and vertical cliffs on the west side of the bay were set with pure stands of large *B. cariosus* 25 to 30 mm high x 20 to 30 mm in diameter with few if any young barnacles present.

An examination of these areas in 1930 showed that the mature *B. glandula* on the east beach had disappeared and were replaced by young *B. glandula*, 4 to 6 mm in diameter, with a few scattered *B. cariosus* in the lower meter. On the west rocks and cliffs all of the old *B. cariosus* were dead, many had been washed off and those remaining were heavily set with *B. glandula* in the first meter and with young *B. cariosus* in the second and third meters.

Reefs at the entrance of this bay were densely covered with both young and old barnacles, with the young *B. glandula* extending well down into the second meter below high tide and attached to the old *B. cariosus*. Star fishes and snails were very abundant in the third (lower) meter and had done considerable damage to the old barnacles in both the second and third meters.

Starfishes were abundant, 3 to 5 per m^2, at the cable crossing, a check station located on San Juan Island, northeast of the Biological Station (station 18), and at Barnacle Rock (Rice, '30; station 5). At both stations they did great damage to the barnacles in the third (lowest) meter level. They actually killed all barnacles on the third meter level at the cable crossing and did considerable damage to those in the second meter. They may help to account for the great differences in abundance of old barnacles in the second and third meters at Barnacle Rock as shown by Table 7.

B. *Barnacle Rock near Olga—Station 5*

Barnacle Rock, a rocky reef near Olga, had next to the largest barnacle population examined within the area of low salinity in 1928. Table 7 shows the change and distribution of the barnacles at each level in 1928 and 1930.

TABLE 7. Comparison of barnacle population per m^2 of Barnacle Rock. Station 5, near Olga.

	1928			1930		
	Mature	Young	Total	Mature	Young	Total
First (top) meter						
B. glandula...........	9,000	4,000	13,000	3,200	37,700	40,900
B. cariosus...........	15,000	5,000	20,000	6,500	48,000	54,500
Second meter						
B. glandula...........	20,000	3,000	23,000	0	45,400	45,400
B. cariosus...........	9,000	1,000	10,000	11,000	14,400	25,400
Third meter						
B. glandula...........	0	0	0	0	0	0
B. cariosus...........	15,500	5,000	20,000	0	21,000	21,000

The following differences are apparent between the 1928 and the 1930 observations: The number of mature *B. glandula* had decreased in the first and second meter levels; *B. cariosus* had decreased in the first and third and had

increased in the second meter; young *B. glandula* increased in the first and second meter; young *B. cariosus* had increased in all levels.

C. dalli covered all areas not occupied by other barnacles in the first and second meter levels in 1930 but was not present in noticeable numbers in 1928. The first trip to this station was made July 1 and a second trip was made August 11 to see what changes had taken place meanwhile. The only difference noticed was the increase in size of young observed on July 1, lack of dead young and the increase in number of 0.5 to 1.0 mm young.

TABLE 8. Comparison of young barnacle population per m² of high salinity and low salinity stations; August 11, 1930.

	STATION 12 High salinity; 30 gm per 1			STATION 5 Low salinity; 28 gm per 1		
	Older Sets 5-15mm	New Sets 1-5 mm	Total	Older Sets 5-15 mm	New Sets 1-5 mm	Total
Top meter						
B. glandula	6,500	3,500	10,000	27,700	10,000	37,700
B. cariosus	1,000	3,000	4,000	40,000	8,000	48,000
Second meter						
B. glandula	6,500	0	6,500	40,000	5,400	45,400
B. cariosus	3,000	27,000	30,000*	18,000	6,400	24,400
Third meter						
B. glandula	1,200	0	1,200*	0	0	0
B. cariosus	4,800	1,200	6,000	11,000	10,000	21,000

A comparison of high salinity station 12 and low salinity station 5 in Table 8 shows that the low salinity station on August 11 had a greater number of survivals and new attachments than the high salinity station except for older sets of *B. glandula* in the third meter, and the new sets of *B. cariosus* in the second meter.

Two-thirds of the young at station 12 were attaching to rock surfaces while three-fourths of those at station 5 were attaching to mature barnacles often piling up to a depth of 15 cm, with the exception of the third meter level; there they did set on bare rock, crowding together making a solid mass 10 to 30 mm high. The moisture-holding and shade-producing properties of the very rough surface account for the different survival of the younger sets during the warm months.

c. *Miscellaneous Observations*

Observations made in 1930 on two low salinity stations, Barnacle Rock (station 5) and Parker Reef (station 3) showed that great changes had taken place since 1928 (Table 9). Great numbers of the old barnacles were dead and had been washed off. Young were abundant but their survival poor

except on the few remaining old barnacles. *C. dalli* was very abundant in all open spaces in the first and second meters.

TABLE 9. Comparison of total population changes per m² in two low salinity stations between 1928 and 1930: Barnacle Rock, station 5; and Parker reef, station 3.

Year	Meter level	Station 5			Station 3		
		Mature	Young	Total	Mature	Young	Total
1928........	1	24,000	9,000	33,000	30,000	11,000	41,000
1928........	2	29,000	4,000	33,000	28,000	8,000	36,000
1930........	1	9,700	85,000	94,700	5,000	10,000	15,000
1930........	2	11,000	59,000	70,800	1,000	7,500	8,500

Such fluctuations in the population of old and young barnacles indicates the importance of annuation in the composition of the community at any one time. A year in which tidal conditions favorable for the attachment of larvae are accompanied and followed by favorable conditions, meteorologic and otherwise, for survival and growth, brings about an increase in the one or more species favored. The large population persists for a period corresponding to the length of the life cycle of the species concerned (perhaps two years) unless in the meantime conditions become especially favorable for barnacle predators. Since especially favorable years may be separated by considerable intervals intermediate periods of small population intervene. Thus in 1928 and the year or years immediately preceding conditions seem to have been especially unfavorable for *Chthamalus dalli* in the areas investigated while conditions in 1929 or early 1930 favored the propagation of this species to the extent that it occupied all areas in which it did not compete at a disadvantage with the already established *B. glandula* and *B. cariosus*.

All shores visited in the region of Bellingham Bay and Samish Flats (stations 21 and 20) showed a heavy attachment of young and old barnacles of all three species through all three levels. The young, 2 to 10 mm in diameter, were mostly attached to the old, often piled up to a depth of 8 to 15 cm.

Apparently, from general observations, conditions were very favorable for seeding throughout the low salinity area during the latter part of June and the first week of July. Those that were fortunate enough to attach to old specimens dead or alive, had a high rate of survival. If there was heavy seeding during the middle part of July the greater portion died. There was a heavy attachment during the first and second weeks of August and few were dead when observed on August 8 and 9.

3. CONCLUSION

The arrangement of the various dominant species of barnacles at any time is the result of attachment, survival of young and death from age. The

series of events and the changes produced by them are significant when the detailed history is known in full. *Without* the entire series of environmental and biological events, local and irregular arrangements often found, can have no significance. This principle must apply to the details of plant arrangement in terrestrial communities and with special force to annuals and biennials.

Rasmussen made observation on this community at La Jolla, near San Diego, California, and his observations were confirmed by observations of the writer at Laguna beach, fifty miles farther north.

B. SOUTHERN CALIFORNIA BALANUS-LITTORINA COMMUNITIES

EFFECTS OF WAVE ACTION AND FRIABLE MATERIAL

D. I. RASMUSSEN

The tidal communities of the Pacific coast have been studied in considerable detail in the vicinity of the Puget Sound Biological Station and the papers of Shelford and Towler ('25), Towler ('30), Worley ('30), and Rice (30) indicate something of the composition and extent of these communities in that region. No corresponding studies have been published on other portions of the Pacific coast, although Shelford ('30) published the results of general observations which he made on the tidal communities from Alaska to Southern California.

The writer spent six weeks during the early part of 1931 in a study of the tidal communities of the southern coast region of California. All areas of rocky shores from Oceanside to San Diego Bay were visited and conditions noted. The most intensive work was done at Alligator Head, La Jolla, Mussel Rocks near Del Mar, and a rocky area along the northern portion of the Scripps Institution grounds. Vertical distribution was best shown on the concrete pilings at the Scripps Institution pier. The areas of shore line within the Institution's grounds provided exceptional advantages, as they have been closed to the collection and removal of any of the animals by the public.

1. GENERAL CONDITIONS

The whole area was not exceptionally rich in rocky shores. The coast line was along the face of eroding cliffs in many places and where rocks were present they appeared to be of a very friable nature which offered a poor foothold for sessile animals. No definite sheltered rocky areas were seen, the coast as a whole being rather uniform and all rocky shores subject to direct wave action. In most localities there was considerable sand present and in movement with the wave action.

Daily records kept at the Institutional pier and supplied me by Dr. Moberg

show an average salinity for January, February and March of 1931 as 33.78 gm of salt per 1 with extremes for the same period of 33.86 to 33.62 gm per 1, determinations made by the chlorine method. Average records for some years past show this to be slightly high, differing less than 0.1 gm per 1, however.

The range of the tides at La Jolla is not as great as that in the Puget Sound region, where most of the work on tidal communities has been done. This difference should be borne in mind in any comparisons.

The mean range of tides at La Jolla is 1.13 m and the extreme range above mean low tide, 1.55 m; at Cattle Point, San Juan Island, the mean range is 1.53 m, and the extreme range above mean low tide, 2.53 m.

This difference of three feet in the diurnal range of the tides means that on similar shores there would be over 50 per cent more area in the intertidal area on the San Juan Island shore than at La Jolla.

2. QUANTITATIVE OBSERVATIONS

Numerous area counts were made of the more abundant sessile animals. In making the counts a frame of 0.10 m^2 subdivided into squares measuring 0.005 m^2 was used. Counts were usually made on areas of 0.25 m^2 but for the smallest of the animals only 0.01 m^2 was used. Counts were made with the idea of covering typical groupings. The usual situation seemed to show two minor communities, appearing as parallel belts along the shore line. In numerous situations the seemingly characteristic animals of these communities were found intermingled with one another. Some species ranged over the entire intertidal area and so the two communities were not entirely distinct. Together they are considered as the Balanus-californianus association. The two modified communities within the associations are here designated as faciations.

The Mytilus-californianus Faciation,—From the lower low tide mean (0 tide) to a height of approximately 1.2 m, on the piling under the pier, was a nearly solid stand of the mussel *Mytilus californianus* Conrad. The mussel appeared as a true dominant, occupying the available surface. The barnacles, limpets, sea anemones and chitons were found living on the shells of the mussel, the crab *Hemigrapsus nudus* (Dana) and a number of small crustaceans in the spaces among the sessile forms. This is perhaps the ideal condition and ideal arrangement. A number of areas of abrupt and durable rocky shores showed the same condition in a lesser degree.

As judged from a variety of situations, the order of attachment on a bare surface appeared to be first the abundant barnacles of the acorn type. These did not necessarily precede the mussels, as mussels were seen establishing themselves on certain surfaces that were practically free from barnacles. The mussels establish themselves on all favorable situations, and many times at

the expense of other animals. There is no order in this replacement that can be interpreted as 'succession.' There were often situations where the starfish had eaten all the mussels from a small area, but other than that there seemed to be nothing that supplanted the mussels. The starfish only preyed upon them and did not take their place in an area.

Along the shore were numerous rocky places near the 0 tide mark in which mussels were not present, except in very small isolated groups. The friable rocks did not seem to afford the right kind of attachment, and other conditions were not ideal. In such situations the lowest part of the intertidal belt had quite a ground work made up of the native oysters, *Ostrea lurida* Carpenter, often covering the rocks completely. In areas near the oysters were the barnacles, *Balanus glandula* Darwin, and the thatched barnacles, *Tetraclita squamosa rubescens* Darwin attaining its maximum development. There were numerous chitons, limpets, small acorn barnacles *Chthamalus fissus* Darwin and the tube mollusk, *Aletes squamigerus* Carpenter. Small compact groups of the goose neck barnacle, *Mitella polymerus* (Sowerby) occurred where wave action was direct, but exposure to the sun slight. The subtidal barnacle *Balanus tintinnabulum californicus* Pilsbry extends upward for 0.5 meter from the subtidal area, in areas that are washed by waves at 0 or minus tides.

Littorina planaxis Faciation,—This is above the community described, that is, reaching from near the mid-tide line to well above mean high tide line, the usual groupings of animals consist of the acorn barnacles as the most conspicuous components. The most abundant species is the very small *Chthamalus fissus* Darwin, often making pure stands, one example showing 524 individuals on 0.01 m^2 or 52,400 per m^2. The usual arrangement on top of the rocks and on exposed surfaces was a stand of the two barnacles *C. fissus* and *Balanus glandula* Darwin at a usual ratio of fifteen to twenty Chthamalus to one Balanus. A single *B. glandula* occupies the equivalent area covered by five to seven *C. fissus*. Shelford ('30) gives the names of *Balanus hesperius* Pilsbry and *B. cariosus* (Pallas) as animals of the intertidal area at La Jolla. There is no doubt some mistake in the locality from which the specimens were taken, as both these species are northern in their distribution and do not extend this far south. (See Pilsbry, '16).

With the two barnacles and also well above high tide line were found the gray littorine, *Littorina planaxis* Philippi. This was very characteristic of the upper portion of the intertidal belt; it was most abundant in rock pockets but not confined to such situations. Numerous limpets, the principal one being *Acmaea persona* Eschscholtz, and the large owl shell, *Lottia gigantea* Gray, were also present, the latter not in any great numbers, but its large size and fairly uniform distribution made it conspicuous. The sea anemone, *Cribrina xanthogrammica* (Brandt) was abundant in the upper community,

but it occurred more often in mats on protected sides of rocks and in the tide pools. As many as 96 were counted in a pure stand on 0.025 m^2 which would equal 3840 per m^2; with this number they formed a complete covering. Their abundant occurrence in many places appeared to be aided by their ability to endure sand in the surf.

3. DISTRIBUTION OF TIDAL DOMINANTS

Numerous counts and studies were made of the animals on the concrete piling under Scripps Institution pier. Animals here showed a greater uniformity than in many other localities, which were seriously interfered with by man and other agencies. The animal population on the pier piling having been protected from disturbance was in many respects nearer that of a natural area than any area along the nearby coast. The greater number and compact arrangement of animals on the piling as compared with adjacent shore, is due no doubt to the more favorable conditions for obtaining food and the comparative freedom from any action by moving sand. The effect of the sand was plainly visible at the base of the individual pilings, both those subject to exposure in an average tide and a very low tide. Table 10 shows the

TABLE 10. Showing the total population of the tidal area based on counts of 0.025 m^2 at 0.166 meter vertical intervals from mean low tide to the upper limits of animals with reading at the maximum (2.1 m) and minimum (minus forty-three hundredths meter) [-.43m] tidal levels of 1931.

Tide range Feet and Meters	*Littorina planaxis*	*Chthamalus fissus*	*Acmaea persona*	*Balanus glandula*	*Lottia gigantea*	*Mitella polymerus*	*Mytilus californianus*	*Cribrina xanthogrammica*	*Balanus tintinnabulum californicus*	Total animals per 0.025 m^2	Total animals per m^2
7.0′=2.1m	0	0	......	......	......	......	......	......	......	0	0
2.0m	2	80	0	......	......	......	......	......	......	82	3,280
	2	170	2	......	......	......	......	......	......	174	6,960
Mean high	5	338	6	5	0	......	......	......	......	354	14,160
5.3′=1.6m	3	270	6	26	1	0	0	......	......	306	12,240
	0	219	5	18	1	17	35	......	......	295	11,800
	......	97	7	9	0	53	14	......	......	180	7,200
1m	......	67	4	11	......	66	7	0	......	155	6,200
	......	138	9	14	......	26	15	1	......	203	8,120
	......	126	2	20	......	18	14	3	0	183	7,320
	......	118	1	13	......	0	16	4	5	157	6,280
	......	123	1	3	......	......	19	3	8	157	6,280
0 tide	......	114	1	1	......	......	17	11	11	145	5,800
(Mean lower low)	......	x	0	0	......	......	x	x	x	x	x
Min. 1931	......	0	......	......	......	......	0	x	x	x	x
Minus 1.4′= .43m	......	......	......	......	......	......	......	x	x	x	x

vertical distribution on squares covering 0.025 m^2 = 6.22 inches on a side. All numbers on the same level across the table occurred in the same square. The vertical columns are for individual species, showing number per 0.025 m^2.

Several counts were made, but this appeared to be nearest average. It is not an average of a number of counts, but a typical count.

The value of this count is enhanced by the fact that the piling has been undisturbed by collecting since its establishment—the mussels here had attained a large size and apparently dominated the area where they were present. All other stands of mussels had been disturbed by bait collectors, etc.

C. Coactions, Reactions and Community Development and Extent

V. E. Shelford

There is undoubtedly competition for space. The chief coactions which are well known are the destruction of barnacles by the snail, *Thais*, and the starfish, *Pisaster*. Much of the feeding is done at high tide. Starfishes and Thais devour barnacles, and mussels are in competition with barnacles for space, but we have seen no evidence that the tidal species are limited downward by predators. The physical factors appear to be the principal control.

Aside from covering the surface with shells there is little reaction on the substratum. Rice, however, found that barnacles attached much better to rock that had been submerged with every tide for a long period than to rocks moved into the intertidal areas from land. This suggests succession.

Miss C. J. Kelley determined the age of several sets of piling in the Balanus-Mytilus edulis area and found that the three principal dominants, *Mytilus edulis, Balanus cariosus,* and *Balanus glandula,* were all present on the piles six months old. Piles one year old merely showed more and larger specimens of the same species. This confirms the findings of Pierron and Huang ('26) and supports the view that there is development without succession in tidal communities (Brandt, '96). Development is also of a short duration.

The life histories of tidal animals are not well known. The life span of barnacles is supposed to be two years. Except for *Mytilus edulis* (Mossop, '22) which reaches six years, other species have not been investigated. Experiments having to do with survival of important species under adverse conditions were referred to under the discussion of the subtidal community.

This community occupies an area bounded roughly at its lower limit by the mean of one-half the lowest tides in each month and at its upper limit by the high tides. It is therefore from two to four meters wide, vertically, but essentially thousands of miles in length. Studies by Newcombe ('35), Appellof ('12), and others indicate similar communities in the north Atlantic

which leads to the suggestion that but one type of tidal community divisible into two or more biomes occupies the northern hemisphere, north to the ice-bound shores. *Mytilus edulis* is the only important dominant common to both the Atlantic and Pacific. The work of Oliver ('23) shows a complete change of dominant species as well as many of the dominant genera in the southern hemisphere about New Zealand. The difference in taxonomic composition between this community and sub-tidal communities is usually sharp. *Balanus cariosus* and *glandula* cease to be present in a sharp line as do all other important species. Subtidal barnacles are fully as definitely distributed and do not (ordinarily) overlap appreciably. Rasmussen found a subtidal barnacle slightly overlapping the tidal species. Gislen ('31) indicates a similar possibility on the Swedish coast.

II. PANDORA-YOLDIA, STRONGYLOCENTROTUS-ARGOBUCCINUM AND MACOMA-PAPHIA BIOMES

V. E. SHELFORD

A. COMPARISONS

Comparing the Strongylocentrotus and Macoma communities, there is the greatest correspondence among the small animals of the plant layer-kelp *(Nereocystis luetkeana)* in one case and eel grass *(Zostera marina)* and allied species in the other. *Margarites succinctus, Lacuna porrecta,* and *Lacuna divaricata* are more abundant, and practically always present on the kelp. One or both of the latter two are often wanting on eel grass and their presence seems to depend upon the eel grass being near the kelp. It is perhaps also favorably influenced by the growth of brown algae on the eel grass. Caprella occurs in abundance on eel grass to which brown algae are attached. On the other hand, the large isopod *(Pentidotea)* is nearly always present on eel grass and almost as often on Nereocystis. On the bottom the ecotone between the two communities is a mere mixture of dominants, usually between 5 and 10m below low tide (Wismer and Swanson, p. 333).

As shown in Figs. 3, 4 and 7, there is a narrow belt of a faciation of the Strongylocentrotus-Argobuccinum biome just below the tidal community area or the Macoma-Paphia biome as the case may be. This is due to the better circulation and wave action that leaves coarse bottom materials exposed and bare.

1. MOTILE ANIMALS

Some marine species, like birds and mammals on land, occur in two or more biomes or move from one to another from season to season. Similarly the marine mammals listed on page 263 and those forms listed below are widely distributed.

TABLE 11. Motile species found in more than one community. A = abundant; C = common; F = few; X = present.

Biome names are indicated by initial letters:	S-A	P-Y	M-P
Liparis pulchellus Ayres	X	C	C
Lepidopsetta bilineata (Ayres)	X	C	C
Psettichthys melanostictus Girard	X	C	C
Pandalus goniurus Stimp.	F	A	
Spirontocaris gracilis (Stimp.)	F	C	X
S. tridens Rath.	X	X	
S. townsendi Rath.	X	X	
S. suckleyi (Stimp.)	F	F	
Crago alaskensis (Lock.)	C	A	X
C. nigricauda (Stimp.)	C	A	—
C. alaskensis elongata (Rath.)	C	A	—
C. dalli (Rath.)	X	C	

B. SERAL COMMUNITIES IN EAST SOUND IN RELATION TO PHYSIOGRAPHIC PROCESSES

A. O. WEESE

1. LOCALITIES AND METHODS

During the summer of 1929 a general survey was made of the bottom fauna of East Sound and adjacent interior waters of the San Juan Island group. The data obtained have a bearing upon problems of marine succession and upon the interpretation of fossil remains. East Sound is a long, narrow, body of water extending into the south side of Orcas Island which surrounds it somewhat in the shape of a horse-shoe. The length is about 12 km and the average width about 1.8 km. The shore line is rugged except at two points, where the villages of Rosario and East Sound are located. The latter is at the head of the sound, which is here divided by a low, rocky headland into two shallow bays, Fishing Bay and Ship Bay. Of these the second is bounded by a sandy beach from which the landward slope is gradual to an altitude of perhaps fifteen meters, followed by a similar downward slope to sea level on the north side of the island at a distance of approximately 2 km. This is the lowest portion of the island and may represent a former strait. The depth of the sound, off shore, varies from twenty to thirty-five meters, but the greater part has a relatively uniform depth of about thirty meters. The bottom material ranges from a very heavy organic mud in Fishing Bay to a mud having a considerable admixture of sand and shell at the mouth.

The principal method of collection was the use of the Petersen bottom sampler, which brings up the surface mud of the sea bottom with the contained animals from an area of 0.1 m^2. The larger, less frequent animals are not accurately represented in the catch, nor are motile forms collected

with any degree of quantitative accuracy. The census of the smaller sessile and inactive forms may be considered, however, as reasonably accurate. In addition, a study of the beach fauna at the head of Ship Bay was made, measured areas being dug up to a depth of 20 cm. The location of the stations at which collections were made is indicated in Fig. 7, and further data are given in Table 12.

Stations 63 and 66 are located in more open waters communicating with the broad Rosario Strait by way of Obstruction and Peavine Passes and more indirectly by way of Thatcher Pass. In the opposite direction communication is with San Juan Channel by way of Upright Channel. Circulation is relatively unimpeded and the bottom material contains a much larger proportion of sand, gravel and shell than elsewhere within the area investigated. The community here may be considered as marking an ecotone between the Strongylocentrotus-Argobuccinum biome (Shelford and Towler, '25) of the regions above mentioned and the Pandora-Yoldia biome (see

TABLE 12. Data in regard to stations at which collections were made.

Station	Height above mean low tide	Character of bottom	Percentage of bottom material retained by 0.2mm. screen	Organic remains identified in bottom material	Remarks
113_1....	1.0m.	Sandy mud	...	....	
113_2....	0.3	Firm sandy mud	...	....	Matted *Enteromorpha*
	Depth below mean low tide				
113_3....	0.1	Sandy mud	...	....	In patch of Zostera
74	20–25	Soft mud	3%	*Coscinodiscus* sp. Foraminifera	Strong odor of H_2S No sand
73	10	Sandy mud	2%	*Coscinodiscus* sp.	Larger particles mostly sand
73_2....	15–20	....	...	....	Not as much sand as 73 No. microscopic examination
72	30	Mud-soft	...	Chaetopterid tubes	No microscopic examination
72_2....	30	Mud—not so soft	...	....	"
71	26	Mud	8	*Coscinodiscus* sp.	
68	24–26	Mud and shell	1	*Coscinodiscus* sp. *Arachnoidiscus* sp. *Biddulphia* sp.	Small fragments Molluscan shells
65	28–30	Mud and shell	3	*Coscinodiscus* sp. *Arachnoidiscus* sp. *Biddulphia* sp. Chaetopterid tubes	Shell fragments larger than in 68
66	24	Mud, shell, gravel	...	Chaetopterid tubes	No microscopic examination
64	36	Mud, sand	32	*Coscinodiscus* sp. *Arachnoidiscus* sp.	Larger particles Mostly sand
63	50	Gravel, mud, shell	...	....	No microscopic examination

Shelford, p. 269) of East Sound. The present paper is concerned chiefly with the phenomena of succession in the latter.

The predominant physiographic processes seem to tend toward land formation at the head of the sound, so that stages of a landward sere may be observed northward from the mouth. Within the sound, deposition of silt is taking place at a rapid rate (see Shelford, p. 266). Quartz sand makes up a considerable portion of the deposit near the mouth of the sound and also, locally (Ship Bay), at the head; molluscan shells also play an appreciable rôle, especially in the outer part, but everywhere organic debris is the most important constituent of the bottom material. Intact shells of larger diatoms may make up as much as 10% of the upper layer.

2. Communities

Census data for each station are given in Table 13, and the relative abundance of the more important dominants in the bottom collections is shown graphically in Fig. 8. Two biomes are represented: 1. The Macoma-Paphia biome; and, 2. The Pandora-Yoldia biome, the latter showing several well defined faciations.[12]

A. *Macoma-Paphia Biome*

The Macoma-Paphia community is characterized by the usual dominants of the Macoma-Paphia association. All the more important dominants are listed in Table 13. Shelford, see page 276, has pointed out that there are many faciations of this community. This one is characterized by *Notomastus pallidior* Chamb. Approximately 5000 annelids of this species occurred per square meter at a level 1.15 m above mean low tide. Shelford did not study the Macoma-Paphia biome in detail, and the annelids of Wismer and Swanson (page 341) were lost enroute to identification which renders comparison difficult. However, the presence of such great numbers of annelids is unusual.

B. *Pandora-Yoldia Biome*

This community has been described by Shelford (see page 266). Most of his studies were made in the area 63, 64, 65, 67, 68, 69 and subordinate stations south of 68. He has characterized the community of this area as the Cucumaria-Scalibregma association. Important species found throughout the area studied (Fig. 8) are *Scalibregma inflatum* Rathke, *Paraprionospio tribranchiata* Berk., and *Macoma brota* Dall. The last named species was represented in the collections by immature individuals only, and is probably an annual. Absent only in the extremely dense mud of Fishing Bay are *Phacoides tenuisculptus* Carp., *Glycinde armigera* Moore, *Amphicteis glabra* Moore, and

[12] Mollander ('30) has used *facies* for the variation of an association characterized by the addition of a species and Clements ('26) has used the same root in *faciation* to indicate the addition or loss of an important species; e.g., Cucumaria-Scalibregma Association—Cucumaria-Scalibregma-Ammochares Faciation.

the Ophiurid *Amphiodia occidentalis* (Lyman). Shelford found this species in large numbers in 1926, but not in 1930. There is evidently a great variation in abundance from year to year. Among the above species are to be found the binding dominants of the association and the various faciations characterizing the area here considered.

(1) Typical Cucumaria-Scalibregma Association.

Stations 64, 65, and 68 may be considered as representing the typical Cucumaria-Scalibregma association. *Cucumaria populifera* (Stimp.) was present in enormous numbers at 64 and 65. However, the individuals collected were mostly juveniles and seemingly represented the results of especially favorable conditions for reproduction. Other important dominants are *Pandora filosa* Carp., *Sternaspis fossor* Stimp., *Phacoides tenuisculptus* Carp. and *Dentalium rectus* Carp.

(2) Diopatra-Chelysoma Ecotone.

Stations 63 and 66, as mentioned above, may be considered as representing an ecotone (Diopatra-Chelysoma ecotone, Shelford (page 269) between the Cucumaria-Scalibregma association and the Strongylocentrotus-Argobuccinum biome. While most of the species found in the typical Cucumaria-Scalibregma association are found also in the ecotone, populations are much reduced and the number of additional species is very large.

(3) Scalibregma-C. piperata Faciation.

Indicated on the map (Fig. 7) in shallow water between the Cucumaria-Scalibregma association and low tide line is a narrow belt in which *Cucumaria piperata* (Stimp.) replaces *Cucumaria populifera.* This faciation is included on the basis of data furnished by Shelford.

(4) Heteromastus filibranchus Faciation.

Beginning with Station 71, there is a progressive dropping out, first of Cucumaria and Dentalium, then of Pandora, Yoldia, *Lumbrinereis bifurcata* McInt., *Natica aleutica* Dall, and others. New species coming in are the annelids *Heteromastus filibranchus* Berk., *Spiophanes cirrata* Sars, and *Spionides japonicus* Moore. This faciation is characterized by the progressive loss of species as one goes up the Sound and an increase in annelid population. *Scalibregma inflatum* is very abundant. *Heteromastus filibranchus* is chosen as the characteristic added species.

(5) Ammochares-Euclymene Faciation.

The annelids mentioned as new dominants in the preceding faciation drop out entirely in the shallower waters of Station 73, and give way to a new group, *Ammochares fusiformis* (Delle Chiaje), *Pista cristata* Muller, *Lumbrinereis latreilli* Aud. and M.E., *Euclymene* (*reticulata*? Moore) and others. The last named species appeared first at Station 73_2. The others occurred

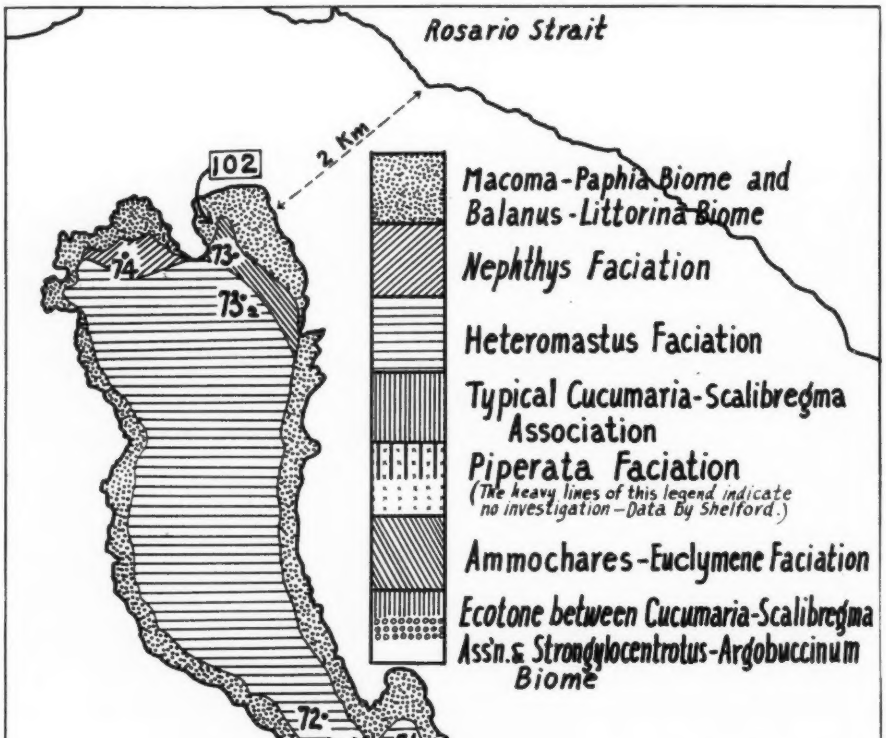

FIG. 7. Provisional map indicating the faciations of the Cucumaria-Scalibregma association (Pandora-Yoldia biome) in and adjacent to East Sound. Either a narrow strip of Macoma-Paphia biome, or the Pisaster ochraceus faciation of the Strongylocentrotus biome occurs between the Cucumaria-Scalibregma association (or its faciations) and mean low tide. The width of both of these is greatly exaggerated. The intertidal area is occupied locally by the Macoma-Paphia biome in its lower edge and by the Balanus-Littorina biome elsewhere. These details cannot be shown, to scale, on this map.

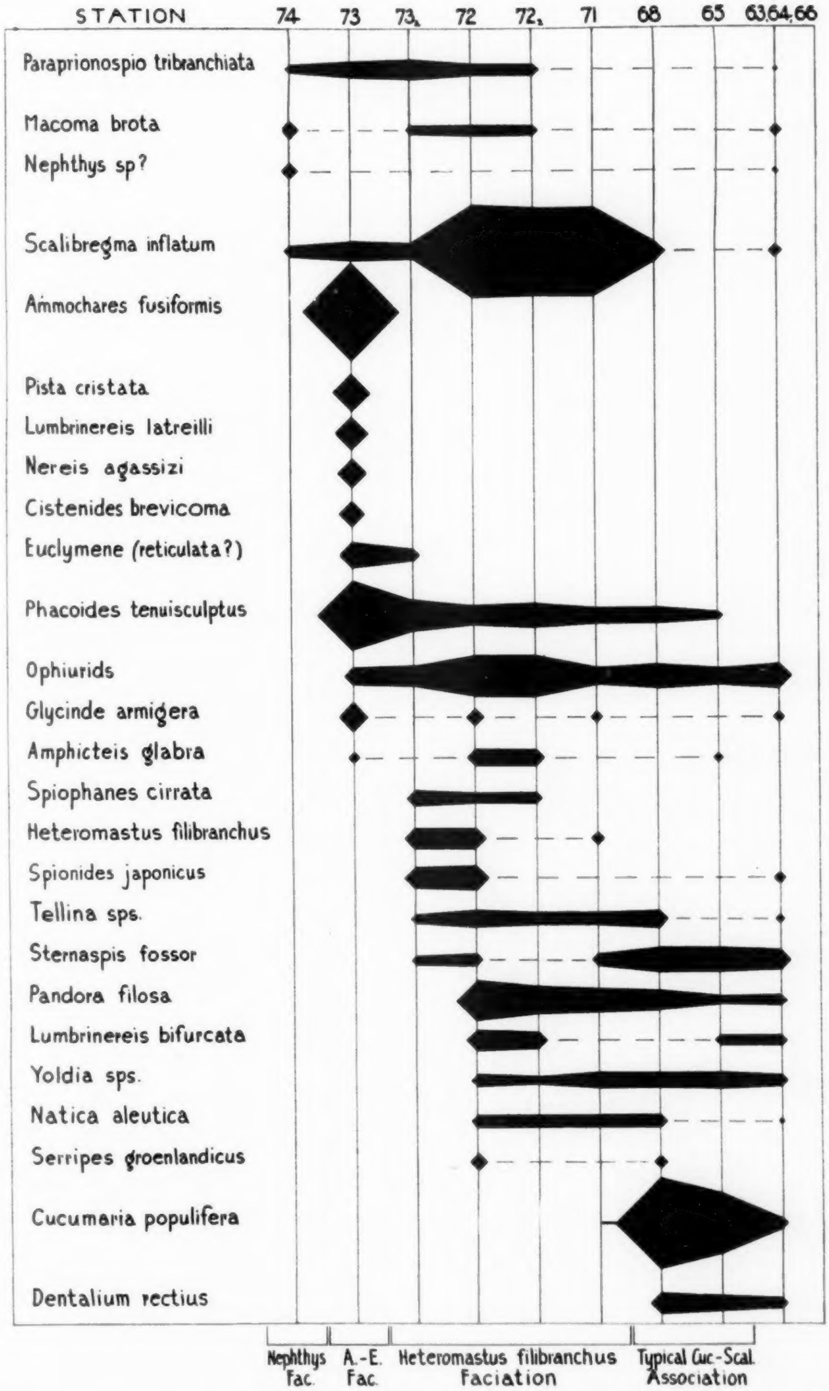

FIG. 8. Showing the distribution of important dominants in the area studied. In order to space the Lohmann[13] spherical type curve in which the width of a black line on the ordinate of a given station is proportional to the cube root of the population at that point. The species here represented are indicated by asterisks in Table 13, where actual populations are given. A. — E. =Ammochares-Euclymene.

[13] Wissensch. Meeresuntersuch. K. Kom., Abt. Kiel, 10:192-194, 1908.

only at Station 73. The area occupied by this community is evidently small and it might accordingly be referred to as a lociation (see Shelford, page 292). The total population here was the largest recorded except that of the upper beach station and the number of species of annelids was largest. The total number of species present was exceeded only at Station 72 and the ecotone stations. *Phacoides tenuisculptus* is also present here in maximum numbers.

TABLE 13.

TABLE 13. Showing the distribution of species and their abundance in the area of study. The table is broken into sections to indicate the natural communities into which the population falls. The figures indicate population per square meter. Asterisks indicate species whose population is represented in Figure 8.

Approximate depth in m below MLT	113_1	113_2	113_3	74	73	73_2	72	72_2	71	68	65	63,64,66
	+1.15	+.5	0.1	22	10	15–20	30	30	26	25	29	24–50
Notomastus pallidior Chamb.	5000	4	....	..	....	....	....	....	....	....	..	......
Macoma nasuta Con.	150	92	50	..	....	....	....	....	....	....	..	......
Macoma inquinata Desh.	24	24	22	..	....	....	....	....	....	....	..	......
Macoma secta Con.	30	2	....	..	....	....	....	....	....	....	..	......
Paphia staminea Con.	14	30	20	..	....	....	....	....	....	....	..	......
Cardium corbis Mart.	10	8	4	..	....	....	....	....	....	....	..	......
Nephthys caeca Fab.	8	22	....	..	....	....	....	....	....	2	..	1
Nephthys hombergii Aud. & M.-E.	......	....	2	..	....	....	....	....	....	....	3	1
Schizothaerus nuttalli Con.	......	26	....	..	....	....	....	....	....	....	..	......
Cardium californiense Desh.	......	8	....	..	....	....	....	....	....	....	..	......
Saxodomus giganteus Desh.	......	6	....	..	....	....	....	....	....	....	..	......
**Macoma brota* Dall	......	....	....	8	....	1	2	2	....	....	..	2
**Nephthys* sp.	......	....	....	8	....	....	....	....	....	....	1	......
**Paraprionospio tribranchiata* Berk.	......	....	....	1	8	17	4	4	....	....	..	x
**Scalibregma inflatum* Rathke	......	....	....	2	16	7	1565	1360	1278	15	..	3
**Ammochares fusiformis* (Delle Chiaje)	......	....	....	..	1692	....	....	....	....	....	..	......
**Phacoides tenuisculptus* Carp.	6	....	....	..	616	57	14	27	8	6	1	......
**Pista cristata* Muller	......	....	....	..	100	....	....	....	....	....	..	......
**Nereis agassizi* (Ehlers)	......	....	....	..	36	....	....	....	....	....	..	2
**Euclymene* (*reticulata* Moore?)	......	....	....	..	34	5	....	....	....	....	..	......
**Cistenides brevicoma* (Johns.)	......	....	....	..	24	....	....	....	....	....	..	......
Scoloplos elongata Johns.	......	....	....	..	18	1	....	....	....	....	..	1
**Glycinde armigera* Moore	......	....	....	..	39	....	6	....	2	....	..	2
**Lumbrinereis latreilli* Aud. & M.-E.	......	....	....	..	62	....	....	....	....	....	..	......
Lumbrinereis impatiens Clap.	......	....	....	..	....	....	1	....	....	....	..	x
Nereis procera Ehlers	......	....	....	..	8	....	....	....	....	....	..	......
Glycera rugosa Johns.	......	....	....	..	5	....	1	....	....	....	..	......
Pectinaria auricoma (Muller)	......	....	....	..	4	1	....	....	....	....	..	......
Ammotrypane sp.?	......	....	....	..	2	....	....	....	....	....	..	......
Glycera tesselata Grube	......	....	....	..	2	....	....	....	....	....	..	......
Phyllodoce sp?	......	....	....	..	2	....	....	....	....	....	..	......
Maldanid	......	....	....	..	2	....	....	....	2	....	1	x
*Ophiurids	......	....	....	..	8	12	143	108	10	25	11	24
**Amphicteis glabra* Moore	......	....	....	..	2	....	10	4	....	....	1	......

(6) Nephthys Faciation.

At Station 74 the population is reduced to a minimum, the only species remaining being *Scalibregma inflatum, Macoma brota, Paraprionospio tribranchiata,* and an undetermined species of Nephthys. Other undetermined specimens of this genus were taken at Stations 64 and 65 but the species is probably not the same. The lack of an accurate determination of this species makes its use in nomenclature of somewhat doubtful propriety, but this community may be called, tentatively, a Nephthys Faciation.

Approximate depth in m below MLT	113_1	113_2	113_3	74	73	73_2	72	72_2	71	68	65	63,64,66
	+1.15	+.5	0.1	22	10	15–20	30	30	26	25	29	24–50
**Heteromastus filibranchus* Berk.						14	12		4			
**Spionides japonicus* Moore						16	27					2
**Spiophanes cirrata* Sars.						8	2	2				
Nereis notomacula Tread.						x						x
Anaitides mucosa Oersted						x						x
Streblosoma bairdi (Malm.)						x						
**Tellina* sps.						1	6	4	4	10		1
**Pandora filosa* Carp.							116	50	24	18	1	2
**Lumbrinereis bifurcata* McInt.							18	6			2	2
**Yoldia* sps.							5	1	6	8	9	4
Psephidia sps.							8			2		x
Lyonsia californica Con.							7					
**Serripes groenlandicus* Gmel.							7			2		
Marcia subdiaphana Carp.							4	2				
Glycera capitata Oersted							3				2	
**Natica aleutica* Dall							3	4	4	4		x
Glycinde sp?							1					x
Ampharete gracilis Malm.							1					
Ampharete arctica Malm.							1					x
Goniada brunnea Tread.							1					
Pilargis berkeleyi Monro**							1					
Glycinde sp?							1					x
Leodicid sp?							1					
Lumbrinereis sp?								10				
Glycera nana Johns.								2				
Leptosynapta sp?							1			21		4
**Sternaspis fossor* Stimp.						1	3		4	26	21	20
**Cucumaria populifera* (Stimp.)										1295	460	2
**Dentalium rectius* Carp.										12	10	4
Capitellid sp?										2		
Nephthys cirrosa Ehlers											2	
Sabellid sp?											1	
Polynoid sp?											1	x
Lima sp?											1	
Total population per M^2†	5276	266	104	19	2683	205	1993	1612	1368	1454	562	132
Total Species	15	19	8	4	26	29	39	23	19	20	23	62
Population annelids per M^2	5016	36	6	11	2058	84	1659	1391	1294	45	35	39
Species annelids	5	5	3	3	20	15	19	9	7	4	10	16

**Ann. and Mag. Nat. Hist., 11:673-675. 1933. †Some species not recorded.

3. Succession

Conditions in East Sound suggest the following successional relationships following the closing of the sound.

If East Sound were at one time a strait it would have been characterized by a Strongylocentrotus-Argobuccinum fauna now typical of large areas of more open waters (Strongylocentrotus-Argobuccinum biome). Important dominants would have been *Strongylocentrotus drobachiensis* Moel., *Argobuccinum oregonensis* Red., *Balanus nubilis* Dar., etc.

A. With the partial closing of the present head of the Sound would have come, with the deposition of organic debris, a transition by way of a Diopatra-Chelysoma ecotone condition to a Pandora-Yoldia fauna.

B. The latter stages of the process after the closing of the head of the Sound involving the progressive deposition of organic debris are evident in the present condition of the area. The typical Cucumaria-Scalibregma association is giving way to the Macoma-Paphia biome through a series of faciations described in this paper, involving a gradual loss of species and an increasing dominance on the part of *Scalibregma inflatum* and other annelids (Heteromastus faciation).

C. Where considerable amounts of inorganic material are added to the bottom material by the outwash of littoral sand the transition to the Macoma-Paphia biome is by way of a faciation involving increased dominance on the part of *Phacoides tenuisculptus* and the appearance of a different group of annelids (Ammochares-Euclymene Faciation).

D. With increased deposition of organic debris without the addition of sand, resulting in a soft organic mud with a high H_2S content, the fauna becomes extremely depauperate, and, as a part of the sere leading toward a mudflat, we have a community which we have designated as a *Nephthys Faciation*.

4. Interpretation of fossil deposits

In favorable localities where bottom materials have not been worked over by wave and current, we should be able to identify successive layers of deposits containing fossil remains of animals representing the communities above named. Stage 1 should be easy of identification with its large number of shell-bearing dominants. Stage 2 would be characterized by the dropping out of such forms as Argobuccinum and Balanus, an increase in organic debris evidenced chiefly by the presence of shells of diatoms, and the appearance of Pandora, Yoldia, Phacoides, etc. The disappearance of these molluscs in turn, with a corresponding change in the character of the soil would indicate the later faciations. It is to be hoped that investigations of this type may be undertaken in the East Sound area. The application of similar methods to the study of fossil deposits elsewhere might be expected to yield results worthy of consideration.

C. EARLY STAGES OF SUCCESSION FROM MARINE CONDITIONS TO LAND

ARCHIE MACLEAN

The area of study includes a small inner lagoon nearly cut off from the larger bay by a gravel bar. This lagoon was almost filled with mud, etc. It may, however, be assumed that this at one time was similar to a small lagoon southeast of Friday Harbor (Newhall's Lagoon) which was a typical Cymatogaster-Haminoea community (see Powers, '20, p. 379; Muencher, 15, Fig. 10, unnumbered lagoon now destroyed by a park development). It did not drain entirely at low tide and had a mud bottom. Newhall's Lagoon, the one studied by the writer and a later stage (station 101) briefly described by H. C. Markus (page 324), constitute a series in which biotic factors dominate in succession.

From the studies of Weese it is made evident that with changes in topography, the change from sea to land communities is initiated in a Macoma-Paphia community. The locality which forms the basis of this paper presented a series of stages different from these described for Fisherman's Bay by Shelford and Towler ('25). It indicates, as has already been pointed out on page 279, that there are probably various successional routes from marine to terrestrial communities. The purpose of this study was to determine the changes in community composition which accompany deposition in nearly enclosed arms of the sea where the growth of saline plants and finally other land plants is beginning in the older portions.

1. LOCATION AND METHODS

The observations were made in August, 1930. The place chosen for this study was the inner end of Wescott Bay, near Roche Harbor, San Juan Island, Washington, termed locally Wescott Creek (Fig. 9). It is almost enclosed and an unusually protected body of salt water. The bay extends inward from the northwest side of San Juan Island for over a mile. Its entrance is very narrow and is also protected by Henry Island. The bay is thus well protected and the inner end is not subject to severe wave action. A ridge of sand which has been thrown up, and on which *Salicornia* has gained a foothold, almost cut off the inner tidal lagoon. The lagoon behind this ridge is completely filled at high tide; at low tide the whole area is exposed. The water drains off through a depression in the ridge.

Substations were established at various levels in front of and behind the Salicornia covered ridge (Fig. 9). The first five substations were located in front of it at 3, 2.6, 2.43, 2.2., and 1.65 m below high tide. Substation 6 was in the run off channel at 1.49 m. Substation 7 was back of the ridge on the mud flat at 1.67 m. Substation 8 was located far back in the area near the land at 1.2 m below high tide.

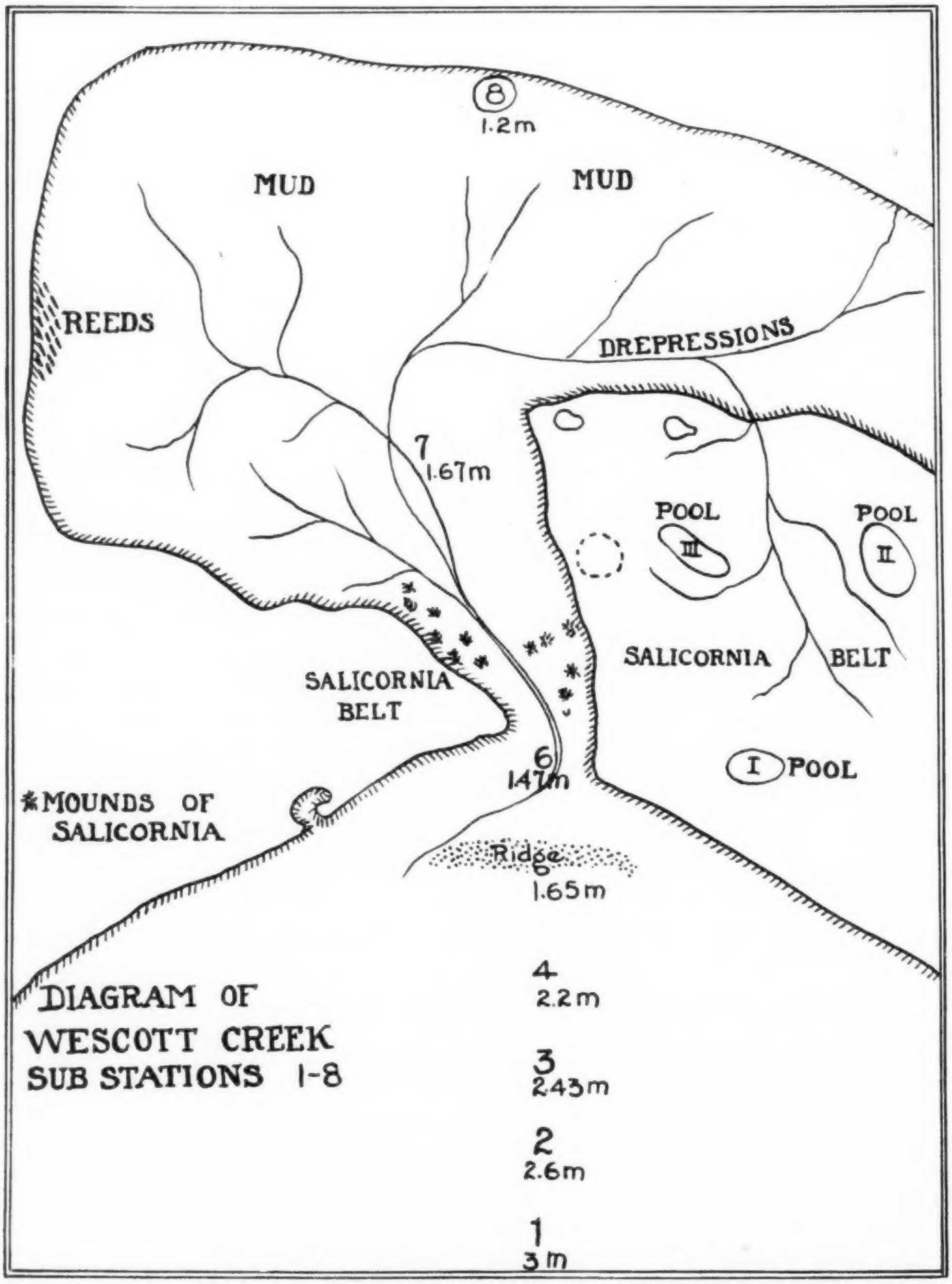

FIG. 9. Map of Wescott Creek (station 101), showing the distribution of study stations, pools, "run off" depressions, and the Salicornia beds.

In the large Salicornia belt were several pools and depressions which were once pools. Three of these, in various stages of evaporation were selected for study (Fig. 9).

Water samples were taken at each station. Three samples were taken on

different days and conditions of the tide. Those referred to in this paper were taken in the morning as the tide was going out. The alkalinity and salinity of the water was noted. The alkalinity was determined with standard acid and methyl orange and calculated as parts per million of calcium carbonate; salinity was determined by the silver chloride method.

Sand samples were collected according to Bruce's ('28) method, and titrated back with sodium thio-sulphate. The hydrogen sulphide was calculated as cubic centimeters per liter.

Two square meters were dug at each station. The sand was turned over with a shovel to the depth of two feet. The specimens obtained were listed for each station and are summarized in the accompanying chart, Fig. 10.

2. GENERAL CONDITIONS; TABLE 14

The alkalinity, in general, increases at each station up to the sixth, dropping to lower levels at the last two stations. The decrease in alkalinity at these stations may have been due to the entrance of fresh water by seepage.

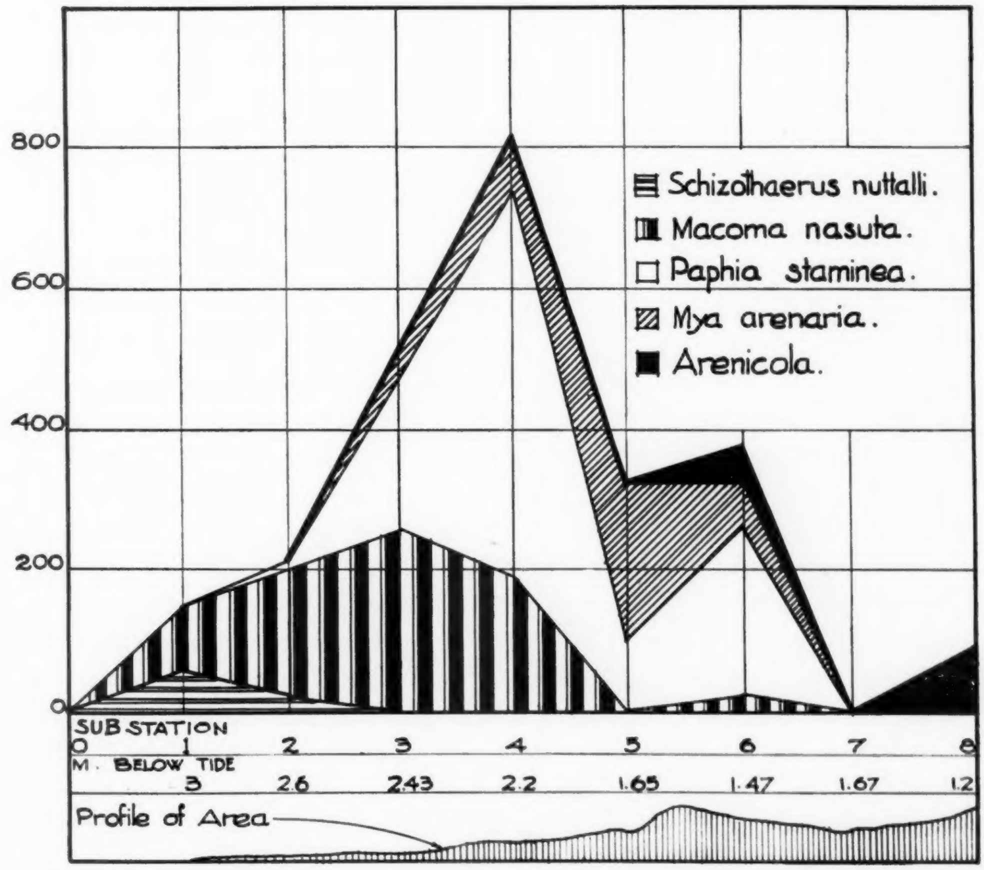

FIG. 10. Showing the distribution of the several important marine animals in the sere toward land.

These stations were nearest rapidly rising land. It will be noted that the alkalinity of the pools became low, decreasing as the water in the pools became less.

The salinity was about the same at each station but shows irregularities to be expected due to the differences in salinity of the different layers of water filling the pool at high tide. One of the three pools in the *Salicornia* belt, however, showed very high salinity as was to be expected.

These pools represented several different stages of depth and evaporation and showed one of the routes of succession to land.

TABLE 14. General conditions at Wescott creek, Station 101 (Substations 1-8 and I-III).

Substations	Meters	Alkalinity	Salinity gm./1	Hydrogen Sulphide cc/1
1	3m	104	29.26	1321
2	2.6m	80	28.51	887
3	2.43m	116	28.00	885
4	2.2m	110	26.61	1747
5	1.65m	130	27.33	2038
6	1.48m	186	29.26	1245
7	1.67m	138	27.55	1411
8	1.2m	114	29.26	1657
Pool	I	126	32.48	....
Pool	II	88	66.83	....
Pool	III	62	25.82	....

The iodine absorption (calculated as hydrogen sulphide) of the mud was very large. It varied at the different stations depending upon the amount of decaying organic material present. At substation 5, which was just in front of a small sand ridge, there was a large amount (2038 cc per 1). Few animals were found here. Apparently large amounts of hydrogen sulphide and organic matter do not make for favorable living conditions for animals. Many dead shells were found at this station. Probably some unfavorable conditions arose which killed off the bivalves.

3. DISTRIBUTION OF ANIMALS

The abundance and distribution of the animals found are shown in Table 15 and Figs. 9 and 10. The last shows *Paphia staminea* to be the abundant bivalve. *Macoma nasuta* next in abundance. *Mya arenaria* is found at higher levels. It will be noted that bivalves were most abundant between 2.4 and 1.8 m below high tide. None were found at substations 7 and 8. Apparently the muddy area, poorly drained and with possible inward seepage of fresh water, is not a favorable environment for them. Most of the bivalves were found in decreasing numbers at the three meter level except *Schizothaerus nuttallii* which increased. S. nuttallii was not found above 2.4 m below high tide.

TABLE 15. Distribution of animals; number per 10 m^2.

Species	Substations							
	1	2	3	4	5	6	7	8
Macoma nasuta	110	180	270	200	0	20	0	0
Paphia staminea	0	30	260	500	100	250	0	0
Schizothaerus nuttallii	60	20	0	0	0	0	0	0
Arenicola sp.	0	0	10	10	10	60	10	100

Specimens of *Mytilus edulis* were found in a few places attached to logs, bearing barnacles. They were of typical shape for this species and fairly large. No small or young ones were found.

Flat muddy areas usually yield an abundance of worms. With the exception of Arenicola, worms were here present in insignificant numbers. Arenicola was found at each of the higher levels back through the mud area.

In the pools scattered over the mud area, the small goby, *Clevelandia ios*, was quite abundant. On top of the mud many small diptera were found, in some areas more than others, twenty per square meter being counted near substation 7.

From all observations, succession to land is taking place here. Physiographic forces are at work. A ridge of gravel has been thrown up across the end of the tide lagoon (Fig. 9). A small new ridge is now being thrown up across the opening. The lack of wave action allows the mud and debris deposited to remain without being disturbed. The water continuing to flow slowly from the back area with each high tide has kept a depression open. As the large ridge remained above the high tide Salicornia gained a foothold, grew and held the sand. Tufts of Salicornia are now appearing on raised portions of the back area. The pools which remain in the Salicornia belt are becoming smaller and drying up.

Pool I contained about two feet of water. It was almost circular and about three feet in diameter. The sides were straight with Salicornia growing up to the edge. Green algae covered the top of the pool. There were many mosquito larvae in the water. Pool II was of similar size. There was only two inches of water in the bottom. Dead Algae covered the bottom and no evidence of insect life was found. A week later this pool was dry. Pool III was larger than the others and was dry except for a small pocket of water near the edge. There were other depressions in which a growth of Salicornia covered the bottom.

The stages of animal succession seem to pass from the Macoma-Paphia association into an Arenicola consocies for at sub-stations 7 and 8 no bivalves were found. The worm, Arenicola, continued back through sub-station 8 which was just in front of the invading land. In this case the Macoma-Paphia association did not remain to the late stages toward land. The

Arenicola consocies gives way to the Salicornia in the lagoon proper and to reeds and tall plants about the edge.

A. In mud bottom portions of the area where there is poor drainage, no bivalves were found.

B. Bivalves are favored by or tolerate a certain amount of organic matter and sulphur compounds (measured in H_2S), but excessive amounts appear unfavorable to them.

C. Worms other than Arenicola were exceptionally few. Arenicola increased in numbers toward the shore. Thus, Arenicola is one of the last marine animals inhabiting the mud.

D. Succession to land proceeds by two routes within this small area: namely, through a Salicornia dominated community on high spots and a rush dominated community around the edges.

D. LATE STAGES OF SUCCESSION TO LAND

H. C. MARKUS

The relations of the Cymatogaster-Haminoea faciation to the invasions of Salicornia is not clear. However, it appears that this plant comes in on hummocks after other plants have dropped out.

A preliminary study of succession from Salicornia to climax forest was undertaken during the month of July, 1930. The observations were made at the inner end of a bay on the north shore of Shaw Island (station 110). A 2000 m^2 area of Salicornia appeared to be growing on a filled pool behind a gravel bar at the inner end of the bay. A small relic pool occurred near the center of the Salicornia area. On its landward side, Salicornia had been succeeded by grasses which covered a belt about four meters wide. Behind this was a forest edge of deciduous shrubs which was being invaded on its landward edge by conifer seedlings of the same species as the trees in the adjacent forest.

The snail *Syncera translucens* Carp. was exceptionally abundant in the Salicornia. Some leaf hoppers occurred but they were more abundant in the grass-covered area. The grasses supported grasshoppers and other insects and spiders. In the forest edge which was invading the grass-covered area, a great variety of land arthropods occurred, some belonging to the same species as the grass inhabitants. Snails and slugs were among the more representative invertebrates of the forest edge. It also presented the usual birds and insects characteristic of such areas in the region.

DISCUSSION

By

V. E. SHELFORD

I. COMPARISON WITH OTHER INVESTIGATIONS

Comparison with communities elsewhere is rendered difficult except in a few cases. The viewpoint and method are usually quite different from ours. In the case of the area exposed at the lowest tides, much work has been done, but usually with much confusion. Tidal and subtidal communities cannot be distinguished on a habitat basis, and have been treated together. The difficulties arising from this fact are aggravated by such conditions are as illustrated by the mixture of the Balanus and Macoma communities described on p. 289. These difficulties can be overcome only by the study of shores on which the communities are clearly differentiated and by the use of a transit to establish contours.

There have been a few important studies of communities on the shores of Australia and New Zealand (Hedley, '15; Oliver, '15, '23), but they differ materially from those of the northern hemisphere and comparisons are not easy. Considering the northern hemisphere where practicable, Appelöf ('12) and King and Russel ('09), Southern ('15) did not organize their observations on a community basis. Allee ('23) used the habitat in his studies at Woods Hole. In the area of his study the shore is low flat with scattered boulders affording a foothold for barnacles, etc. The difficulties are greater than in most localities, but doubtless the use of a transit to determine exact levels and studies elsewhere where the rock areas are of some size would help bring out the community relations more clearly. Beauchamp ('23) used the habitat as have many others. Colton ('16) recognized and differentiated communities on the coast of Maine. His littoral formation is not a formation but concerns the entire tidal region. "Formation" is entirely misused. Pearse ('13) refers merely to zones and considers the plants as a part of the habitat. The remaining work done on American waters including extensive work by the U. S. Bureau of Fisheries was not quantitative and was usually treated according to taxonomic groups, which resulted in a minimum of value from the standpoint of communities.

Investigators attempting to interpret the distribution of organisms are divisible into three classes: (1) Those who use the habitat; (2) those who stress large units and their subdivisions; (3) those who emphasize small units, frequently to the neglect of larger ones. The second group represent the view taken in the classification presented in this paper, which is similar to that of Petersen. There is a slight difference in the views of the large unit users however, some considering the biome or formation as the fun-

damental unit and others its first subdivision, the association (large unit sense). Both groups, however, recognize the same units.

The work of Petersen and his associates who recognized large units is noteworthy in three respects. First, Petersen did not start out to study communities but says they were forced upon him by his researches. Second, he and his associates used accurate quantitative methods throughout long periods. Third, their arrangement of communities is entirely parallel with those of the plant and animal ecologists, who use large terrestrial communities as fundamental units.

Petersen ('14) combined his smaller communities to form larger communities which are entirely comparable to the formation or biome (1915a Supplement to the 1914 annual report, with map). He drew a generalized map of the bottom communities of the North Atlantic based upon a study of the literature for the Atlantic in comparison with the work which he did himself. He combined several of the smaller communities which he had described to make the larger more generalized community. For example, Petersen combined (a) the *Brissopsis-Amphiura* communities (association), (b) *Echinocardium-Amphiura* community (association), (c) the *Haploops* community (faciation), and (d) the *Brissopsis-Ophioglypha* (association) to make the Brissopsis community (formation). The binding dominants are *Brissopsis lyrifera, Abra nitida, Axinus flexosus, Nucula tenuis, Ophioglypha albida, Leda pernula, Balanoglossus kuppferi, Leda minuta,* and *Pectinaria auricoma,* which are found in two or three or more of the four lesser communities (associations).

Petersen also recognized a major community (formation or biome) called the Venus community, covering much of the North Sea and bottom around the British Isles with an extension northward toward Iceland. Sparks ('29) examined the communities about Iceland and the Faroes and confirmed most of Petersen's anticipations. On about 50 km², Ford ('23) recognized the associations of the Venus community and found an additional community of different composition.

Davis ('23) finds the Venus community (biome) of Petersen covering the Dogger Bank in the North Sea. Still further paralleling of plant community phenomena on land is illustrated here. The Bank is characterized by "patches" in which the bivalve *Spisula subtruncata* is 10 to 20 times as abundant as any other species. It thus constitutes the chief dominant and presents a condition parallel to that found in the plant groupings called consociations.

The method of recognizing and designating communities is in strict accord with that of a large group of British and American plant ecologists. Clements' treatment ('20, p. 114) of the grassland, resulting from very similar

facts serves as an example. The writer shows Petersen's terminology in the foregoing statement with that used in this paper in parenthesis.

The work of two Swedish investigators, Gislen ('30) and Molander ('30), was done from the small unit viewpoint. The work of Gislen covers the epibioses of the Gullmar Fjord. These are the biotic communities on hard bottom. This paper includes an excellent and comprehensive summary of the history of the subject. Gislen presents some forty "associations" based on similarity of growth form. He follows the usual practice of algologists in calling every patch of different alga covering a square meter or less, a different *"association."* He refers frequently to sociological relations indicating that his viewpoint is primarily that of a plant sociologist.

A second Swedish investigator, Molander, has also investigated the Gullmar Fjord which Petersen studied and mapped in 1918. His viewpoint appears to be that of the small unit group. Possibly Molander's work was done in greater detail than that of Petersen. Petersen's map shows the following five communities: (1) Macoma; (2) Syndosmya (Abra); (3) Venus; (4) Echinocardium-filiformis; and (5) Brissopsis-chiajei.

On this area of 12 km^2 Molander recognizes nine associations, and including the faciations of these, a total of thirteen communities. He makes four or five communities out of the faciations of Petersen's ('18) Brissopsis-sarsii community (on clay bottom, depth 56-100 m). He further recognizes Petersen's Brissopsis-chiajei community and divides it into faciations; also Petersen's Echinocardium-filiformis community which he divides into three faciations. He also named an additional community which he designated in his introduction as quite distinct and different from others but which he says on page 33 is suggestive of Petersen's Echinocardium-Venus community.

Those animal ecologists who begin with the smallest units are usually students of the social insects or those who have studied the groupings of gregarious and other aggregating animals. A group of twenty-five Paramoecia is an aggregation, but has only a few social values of a herd of 10,000 or 1,000,000 bison, or a school of 100 sperm whales. Among students in this field, aggregation, association, society, colony, etc., are used quite often interchangeably, but usually in senses quite different from those indicated in this paper. Community, which is the accepted ecological term to apply to all of these, is rarely used.

The question of the use of the habitat or of communities, characterized by uniformly distributed species of size and importance in the description of the arrangement and distribution of organisms, is not being much debated at present. The use of the habitat is not supported by present investigation. It is, however, worthwhile to note Petersen's ('13) comments on this subject:

"At first it was thought possible to determine these zones by the depth alone or by a characterization of the vegetation and bottom conditions *(Pruvôt)*, but though much has been gained along these lines we do not hereby come to the kernel of the matter, namely, the occurrence of the generally distributed animals, which alone can tell us where a certain animal community belongs, even though the depth and outer conditions may vary.

"Not even my own previous, laborious charting of all the different species in the Kattegat (Hauch) answered my purpose, partly because in this way I lost the general perspective and partly because dredges were used and all determinations of quantity had to be given up; but I had clearly realized the enormous difference between the various communities and have ever since sought for a method of characterizing the communities in a more synoptic manner that could be easily understood by others. I am now of opinion that I have found it (through the characteristic animals). . . ."

The findings of Huntsman ('18) concerned the distribution of animals, essentially tidal as a rule, near St. Andrews at the mouth of the Bay of Fundy. Balanus, Littorina and Mytilus are distributed over the center 5 m of the 8 m tidal range. The lower edge of their zone is overlapped for 1.0 m by Asterias, Strongylocentrotus and Buccinium. On the St. Lawrence side of the Cape Breton Island, Balanus, Mytilus and Littorina extend throughout most of the 1½ m tidal range and to a depth 18 or 36 m or more. Buccinium is restricted below 36 m and Asterias and Strongylocentrotus are few in number above this level.

Huntsman concludes that the peculiar conditions on the west shore of Cape Breton Island are due to the warm surface waters. He suggests that the barnacles and mussels do not go deeper near St. Andrews because of destruction by echinoderms and welks. The predator view as regards barnacle distribution is not supported by conditions about the San Juan Islands. *Balanus cariosus* and *B. glandula*, and *Mytilus edulis* do not extend below mean low tide. The place of the intertidal barnacles is taken by four or five other species. The same is true on the California coast. In the main body of the Strongylocentrotus-Argobuccinum community about the San Juan Islands starfishes are uncommon and could hardly affect the lower limit of Mytilus. Sea urchins are plentiful and are unlikely to distinguish species of Balanus (see pp. 281, 301, 308, and 309).

The question of controlling factor becomes of especial interest in this connection because of comparisons made possible by the studies of communities of the North Atlantic, Western Europe and Hudson Bay (by Shelford). Comparing all of these with Puget Sound one must conclude that the inferences which may be made at one place are likely to be contradicted at another. The truth is difficult to ascertain without the introduction of experimental methods along with the observations.

In this paper the writers have organized the discussion along lines which have stressed the principles governing the larger community units. They

have used important groups of species as indicators of conditions and of community limits. This is a distinct digression from the viewpoint from which most investigation in American waters has been conducted. The writers, however, believe that this is the most promising method of attacking the philosophic problems of nature as well as those of an economic bearing. The close parallel between the general phenomena brought out in the classical work of the Danish Biological Station and the work of plant ecologists is a further justification for the methods followed.

II. Summary of Conclusions

(1) Two subtidal communities of major rank (biome) occur in the area of study, one a large gasteropod-echinoderm community, the Strongylocentrotus-Argobuccinum biome (p. 280), associated with the more rapidly circulating waters, higher salinity, greater light penetration and less plankton, the other an annelid-bivalve community, Pandora-Yoldia biome (p. 265), in lower salinity, less circulation, slow fine silt deposition, and much bottom detritus. These general hydrographic conditions overshadow the type of bottom in determining the character of the community.

(2) The large bivalve-annelid community, Macoma-Paphia biome (p. 272), which is characterized by edible clams, is essentially subtidal though exposed at the lowest tides throughout its upper third. The success of the clams in its upper third and the height to which they occur is determined by the water holding capacity of the beach sands (also by inference from Danish communities, their size and abundance, by lack of destruction by fishes).

(3) The barnacle-mussel community, Balanus-Littorina biome (p. 289), which begins near mean low tide and reaches to a vertical meter or meter and a half above the upper limit of the Macoma-Paphia biome (mean high tide) is strictly tidal. Its presence is governed almost as much by water movement as by substratum as mussels may form a bed in still water on the upper portions of a sand beach and constitute a substratum for the attachment of barnacles. They thus build up the entire community. This leads to a mixing and competition between the Balanus-Littorina and Macoma-Paphia biomes (p. 289).

(4) The pelagic community (including both plankton and nekton) has an important effect on the subtidal communities chiefly in influencing the penetration of light and the amount of detritus supplied to the bottom (pp. 259, 265, 266).

(5) The evidence gathered from all sources indicates that the general hydrographic conditions (submarine climate) are more important than kind of bottom materials in determining the character of benthic communities (p. 290, see also p. 345).

(6) The arrangement of species on the bottom especially in the Balanus-

Littorina biome is controlled by seeding and survival in relation to combinations of tide, temperature and sunshine. The exact arrangement has significance only when taken together with the series of events producing it. It is quite inexplicable and without significance when approached without details as to preceding events. The observations of Rice demonstrated this for tidal barnacles (p. 293). Variations in the relative position of maximum abundance for the various clams on different beaches and in different years suggest the same relation for them. The same principle probably holds good for the strictly subtidal communities (see 7 below).

(7) The quantity per unit area of any or nearly all the species in the communities studied may fluctuate from season to season, from year to year, or over longer periods. Argobuccinum was very abundant in 1922 when the original work on the Strongylocentrotus-Argobuccinum biome was done. By 1926 it was almost absent but gradually increased to 1930 when observation ceased. In the Pandora-Yoldia biome there was a decline in numbers of Pandora, Yoldia, and Marcia and an increase of Scalibregma (p. 271). The behavior of several other species is similar.

(8) Succession or development of communities has been but little studied. The period of development of Balanus-Littorina communities is evidently not longer than the few months suggested by Pierron and Huang. (Rice found, p. 295, that barnacles do not set well on stones that have not been in sea water.) Development of the Macoma-Paphia biome is evidently rapid on sand beaches (p. 278). Succession is evidently slowest where suitable soils or other substrata must be built up with the aid of organisms, *e.g.,* in the Strongylocentrotus-Argobuccinum biome where a bottom of shells must be built on mud or sand bottom (p. 288) and the Pandora-Yoldia biome, a bottom of mud with much detritus is necessary. All the communities studied are characterized by short life histories and rapid replacement; hence, also rapid development and quick response of community composition to minor changes in external conditions. Most of the communities studied are essentially climax.

(9) The study of East Sound, which is evidently being slowly filled chiefly with organic detritus, shows the large effect of hydrographic conditions in the production of much plankton, etc., and the accumulated reaction of organisms on the habitat with resulting changes in community composition. It is evident that the suggested closing of a passage shutting tidal circulation out of the sound could change hydrographic conditions so as to produce all the noteworthy differences between the communities in the upper end of the sound and the Strongylocentrotus-Argobuccinum biome north of Orcas Island (pp. 312 and 318).

(10) The writers are convinced that organisms, or more especially community groupings of organisms, are the best indicators of hydrographic con-

ditions (submarine climate and weather) and that the success or failure, presence or absence, scarcity or abundance of these living things is correlated with determinable physical and chemical conditions. To yield the best results, the study of conditions and of communities must go hand in hand, but also the nature of the study of conditions must constantly be moulded by a study of the correlation of the responses of organisms with the knowledge of conditions already gained. In other words, biological oceanographic research should not be planned and executed as a technological or engineering project. Beyond a certain point and also probably even at the beginning so-called physical oceanography must take account of the responses of organisms and use them as guides in elaboration of the program. When their responses are understood organisms may be used to extend the generalization of a purely physical survey. The bottom communities are fully as important in this respect as pelagic ones. We are convinced that certain combinations of intertidal species may be used to indicate average salinity of the surface waters (Fig. 1 and p. 290).

(11) The necessary background for pursuing ecological work in the sea cannot be acquired in laboratories or in specialized courses dealing with particular groups of marine organisms. If oceanography is to progress, men will have to be trained through a broad general contact with the physical and chemical conditions and the occurrence and responses of organisms. Instruction of this type is rarely available.

(12) The geographical extent of the major communities is relatively unknown except for the Balanus-Littorina biome.

A. *Balanus-Littorina Biome*

General circumpolar occurrence of Mytilis edulis as an important dominant in parts of the North Pacific and entire Atlantic, and the similarity of dominant life forms, general equivalence of species in both the North Atlantic and North Pacific leads to the conclusion that communities of the Balanus-Littorina biome type cover much of the suitable shores of the northern hemisphere. They are divided into several associations, each with several faciations. The southern hemisphere apparently has different communities.

B. *The Macoma-Paphia biome* (p. 277) is evidently not found in the Atlantic. According to Newcombe ('35) Mya and Nereis are the dominants in the Bay of Fundy and Venus is important farther south. *Mya arenaria* was introduced into the Pacific and while *Macoma balthica*, an important species in Europe, occurs in the area it is of secondary importance. Communities of the general type of the Macoma-Paphia biome occur over the northern hemisphere at least.

C. *The Strongylocentrotus-Argobuccinum biome* (p. 287) is evidently

a North Pacific community. Echinoderm-large gasteropod communities occur, however, in the Atlantic. The communities of Vineyard Sound apparently approach this type.

D. *The Pandora-Yoldia biome* (p. 269) is also evidently limited to the North Pacific. The Abra (Syndosmya) community near Denmark is of this type and it is also probable that one occurs in Buzzards Bay (Mass.).

(13) The tension line between the terrestrial and marine communities is usually associated with the Macoma-Paphia biome. Successions to land occur in nearly-cut-off pools. There are probably several routes to land communities but the invasion of Salicornia on high spots leading to hummocks of Salicornia followed by sedges and grasses is common (pp. 319, 324).

(14) The physiological characters of the animals of the various communities differ strikingly in accord with (a) the general conditions of community habitat and (b) the habits as regards the level occupied by the species (pp. 264, 271, 279, and 289). (See also Shelford, '16.)

(15) Studies of the resistance of animals of different ages (Andrews, '25) and the researches of Rice (p. 295) indicate that life history studies should be carried on under controlled conditions. They should be accompanied by experimental investigation of the sensitivities of the different stages. Field researches which correlate the ever changing physical, chemical and biological conditions of the habitat with the status of species of importance in the communities in question must form the guide for experimental work both out of doors and in the laboratory, *i.e.*, the responses of organisms and not imitation of physical and chemical methods or the easy operation of commercial devices should dictate the experimental conditions imposed.

PART II

A STUDY OF THE ANIMAL COMMUNITIES OF A RESTRICTED AREA OF SOFT BOTTOM IN THE SAN JUAN CHANNEL[1]

NETTIE M. WISMER,
Lawrence (Kansas) Junior High School

and

JOHN H. SWANSON,
Edinburg College

I. INTRODUCTION

The bottom communities of the San Juan channel and adjacent areas have been reported upon by Shelford and Towler ('25), and also by Perry ('16) and Essex and Steggerda ('25), who restricted their attention to hard bottom communities. Shelford (p. 258) surveyed the biomes about the San Juan Islands and reported a new major community on mud bottoms near Olga and the mainland.

In 1926 the writers made a detailed study of the animal population of a restricted area, see station 51, Fig. 1, p. 254, which lies within the hard bottom region previously surveyed by Shelford and Towler ('25). The purpose was (1) to throw light on the distinctness of two major communities, the Strongylocentrotus-Argobuccinum and the Pandora-Yoldia communities, (2) to determine the relative importance of the character of the bottom as compared with the physical and chemical qualities of the water above it, (3) to ascertain the community composition in and on mud bottom, as compared with that associated with the rocks in the adjacent areas, and (4) to establish the lower limits of the clam beach community (Macoma-Paphia biome) which Peterson ('18) has said would reach 30 meters if it were not for competition.

The area studied was 195 meters wide and 377 meters long. It extended from the shore of Brown Island toward the present station site, terminating in mid-channel (Fig. 11). The southeast and south corners were identified by means of points on the shore, while buoys were anchored to mark the north and northwest corners.

The contour of the bottom was determined by soundings and readings from a meter wheel which operated in connection with the bottom sampler cable. A contour map was prepared from the assembled data (Fig. 12).

The nature of the bottom of the area of study was determined from materials brought to the surface by the bottom sampler and dredge. The quality of the bottom and the distribution of most of the plant life is indicated in Fig. 13. It was composed primarily of mud and fine sand with a few shells

[1] Contribution from the Lawrence, Kansas, Junior High School, the Science Department, Edinburg College, Edinburg, Texas, the University of Illinois, and the Puget Sound Biological Station.

and pebbles included locally. Occasionally small boulders were found, especially in the areas containing kelp (Fig. 13). The bottom of the north corner was composed of black mud and molluscan shells.

A few outcroppings of rock were encountered in the 12 to 16 meter levels. The collections from the rocks did not include the important species from

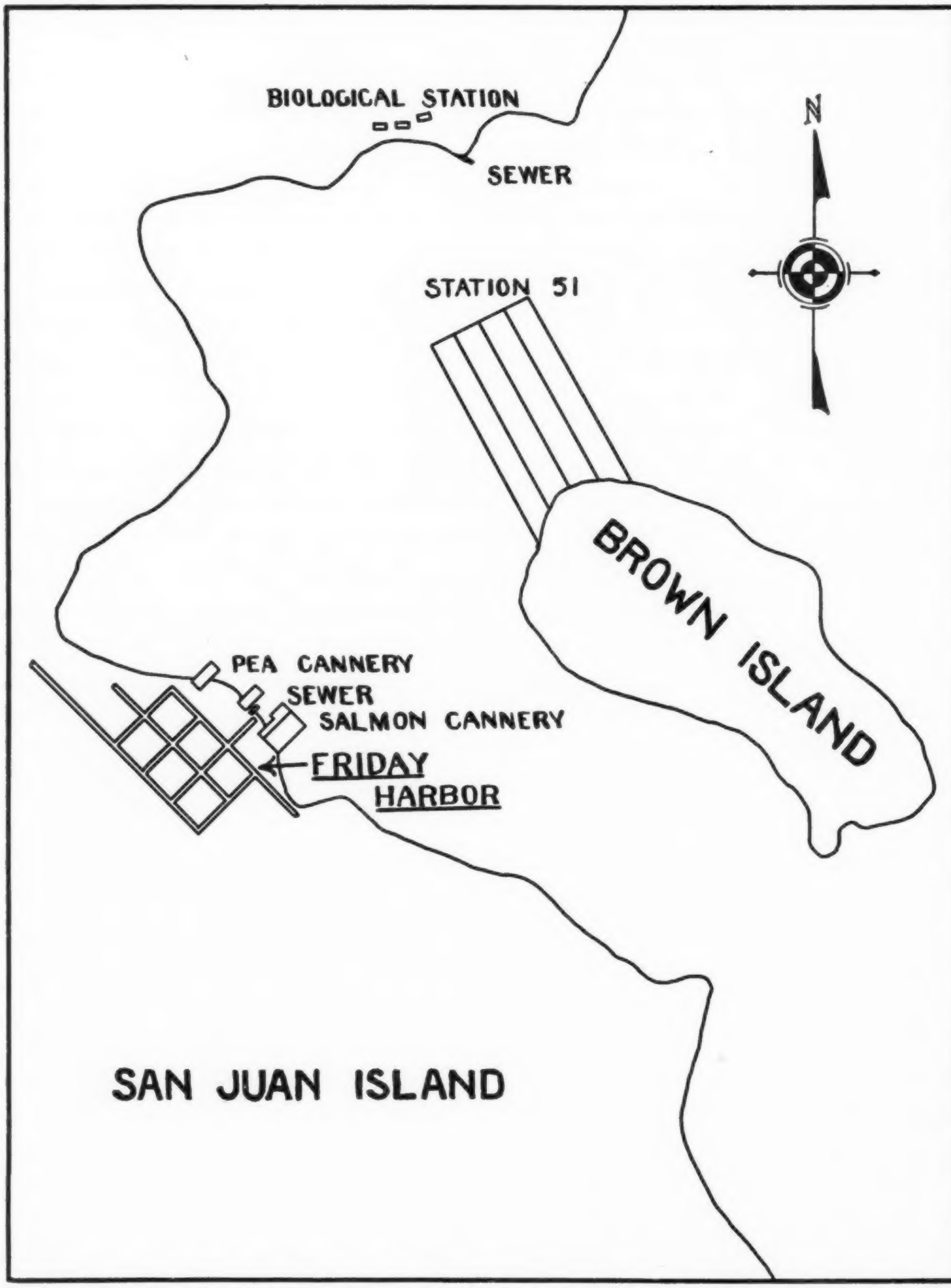

FIG. 11. Showing the location of station 51 in relation to Brown and San Juan Islands.

which conclusions are drawn, except for two or three individuals. The remainder of the rock collections were of no particular ecological significance due to their infrequent occurrence.

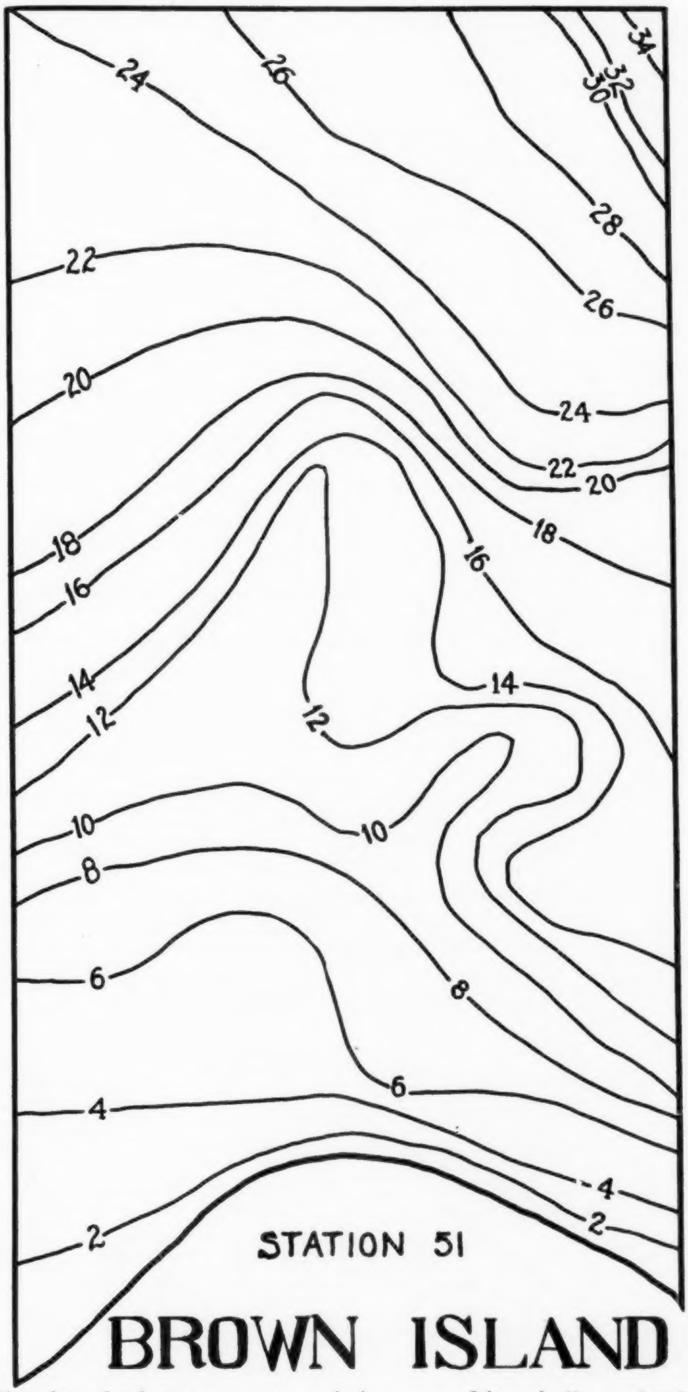

FIG. 12. Showing the bottom contour of the area. Lines indicate depths in meters, measured from mean low tide.

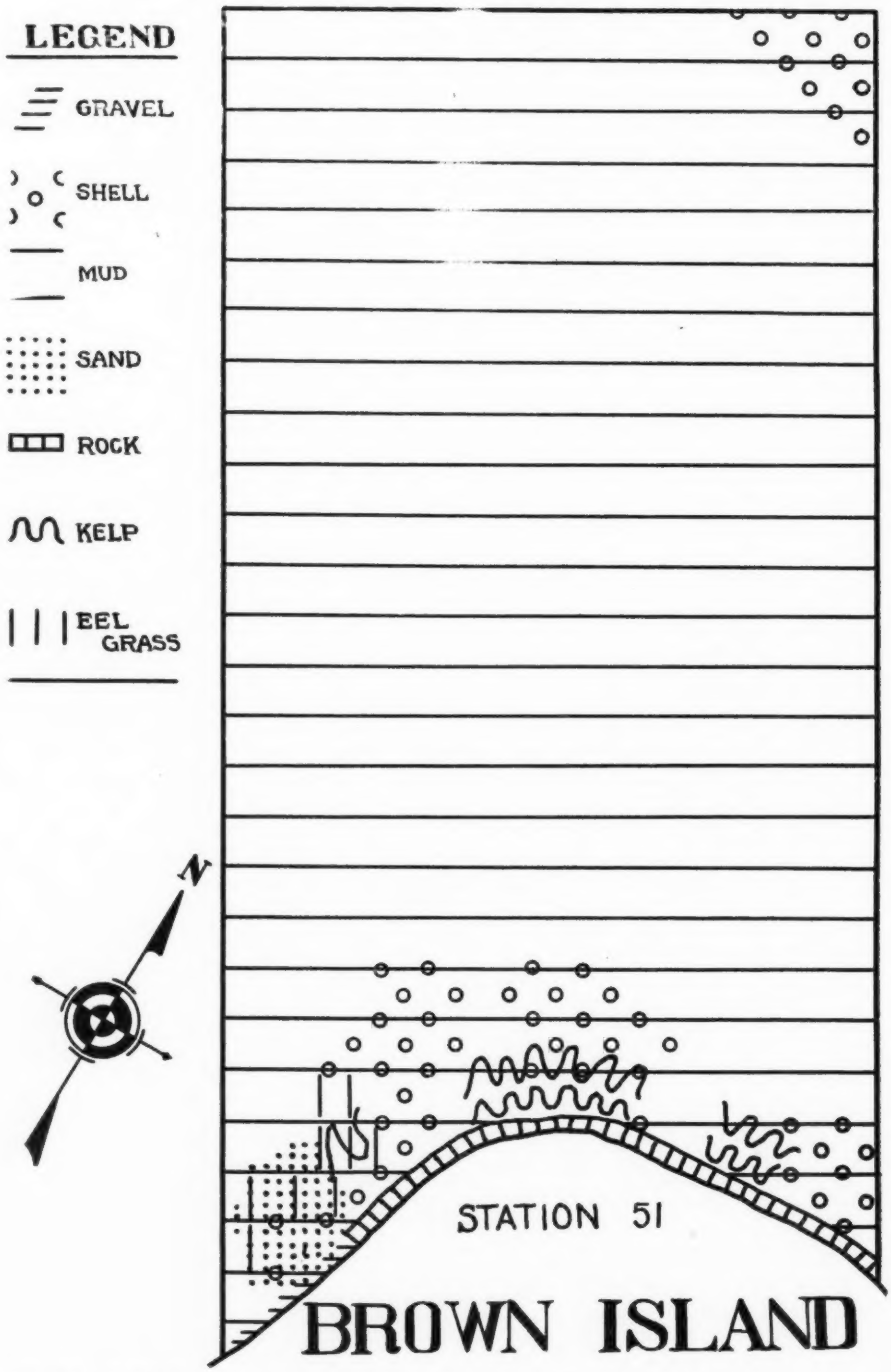

FIG. 13. Indicating the composition of the bottom and the distribution of kelp and eel grass within the area studied.

A considerable amount of Nereocystis (kelp) was found at two to six meter depths, especially off the rockier portions of the shore. Detached fronds or whole plants of other species of algae were encountered below a depth of twelve meters. Zostera (eel-grass) was abundant in a restricted area in the south corner.

The shoreline was rocky, especially in the 1 to 1.5 m between the upper limit of clams and high tide. This belt was partially covered with barnacles and harbored many motile tidal species. No account was taken of this belt.

(1) Methods of collecting and determining number of specimens.

A measured total of one square meter of sea bottom was brought to the boat's deck at each of fifteen substations (I-XV, Fig. 14) by means of a Petersen bottom sampler of 0.1 m^2 capacity. The organisms were washed free of mud and detritus in 2 mm mesh sieves.

Kelp holdfasts totaling 1.5 square meters were dislodged from the bottom by pulling on the plants from the stern of a rowboat. The surface area of stones, etc., brought up in this manner was measured with a ruler.

A naturalists' dredge and a trawl were towed over various parts of the area (a-p, and 1-3, Fig. 14). The dimensions of the dredge frame were 1.15 meters by 0.55 meters. Those of the trawl were 1.9 meters by 0.5 meters. Both nets were of one inch mesh. The distance over which these instruments were towed was estimated by noting positions of the boat in relation to various points on the shore.

TABLE 16. Showing efficiency of dredge and trawl at various stations.

Dredge		*Trawl*	
Haul	Per Cent Efficiency	Haul	Per Cent Efficiency
a.	4.57	1.	41.35
e.	0.29	2.	1.53
g.	0.63	3.	0.52
j.	4.56		
k.	0.53		
l.	1.30		
n.	8.47		
p.	0.89		

Average efficiency, 2.65 per cent.

The efficiency of the dredge and trawl was estimated at various stations by comparing their catches of non-motile or slow-moving species qualitatively and quantitatively with those of the bottom sampler for the same area and averaging all values thus derived for these species. The sampler was assumed to be 100 per cent efficient (Kirsop, '22, has estimated it to be 95 per cent efficient on mud bottom). An average efficiency of the dredge or trawl for the entire plot could have been estimated by assembling all efficiency data according to species and without reference to stations. The value for average trawl efficiency used in this study was derived by averaging all calculated station values. It is 2.65 per cent. This estimate was used in computing the number

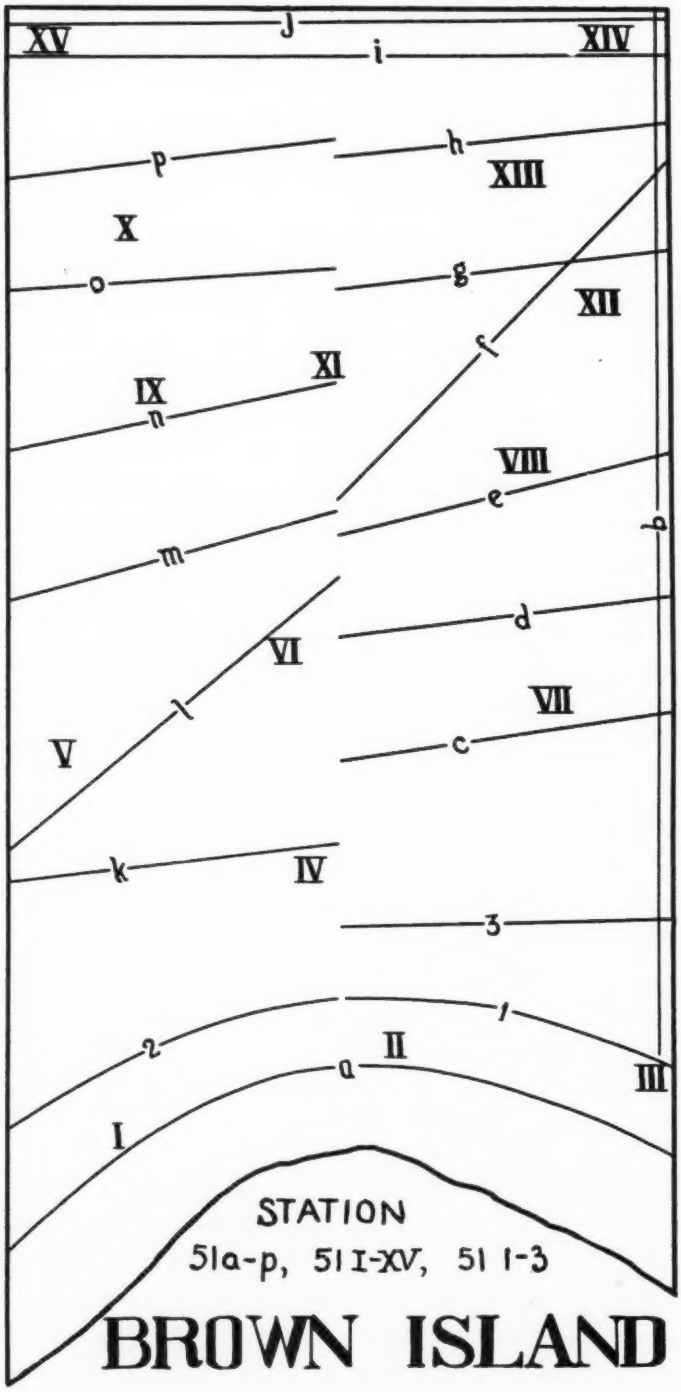

FIG. 14. Showing location of the substations of station 51 for the use of the various instruments. Letters (a-p inc.) refer to dredge hauls; Roman numerals (I-XV) refer to bottom sampler stations; Arabic numerals (1-3) indicate hauls made with a rock trawl.

of animals at stations where a very small number of non-motile forms were collected by the apparatus.

The high efficiency of the trawl at station 1 as compared with that at stations 2 and 3 is referable to differences in the amount of vegetation encountered. Many animals living at the depth represented by station 1 are found in and on vegetation and they readily fall into the collecting device. In comparing stations 2 and 3 it must be remembered that as depth of the water increases the pull of the cable becomes increasingly effective in causing the instrument to skip over specimens.

The efficiency of the dredge at various stations is seen to vary within a wide range (Table 16). This is referable to (1) differences in relative length of cable let out while the instrument was in tow, (2) differences in the slant of the sea bottom in relation to the direction of pull of the cable; a dredge will usually collect more effectively if it is pulled up a slope than if it is pulled down one, and (3) the amount of vegetation encountered. Thus at substations *i* and *n*, where vegetation was denser than at all other relatively deep water points, the values for efficiency were higher than at any other outshore stations at which an estimate was made. Despite the presence of vegetation at lower levels, especially at the above stations, there is evidence to support belief that efficiency decreases slightly with depth, as may be seen in Fig. 15.

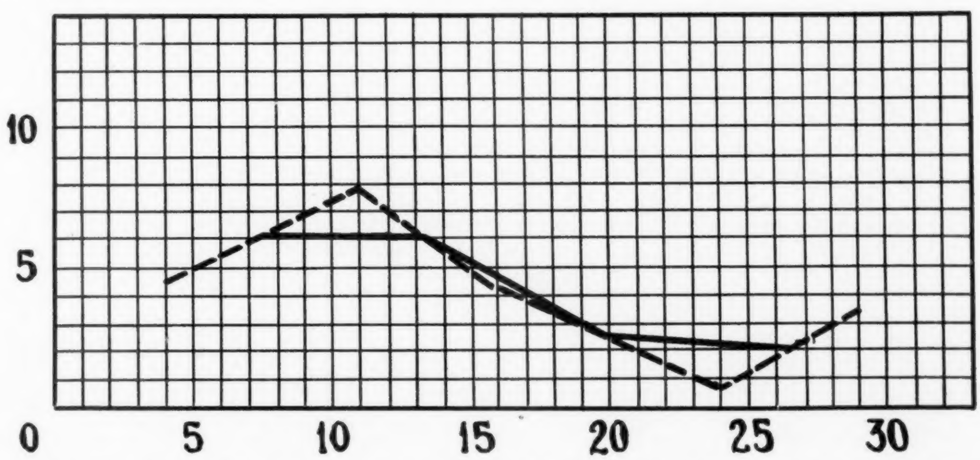

FIG. 15. Showing efficiency of the dredge plotted against depth. The broken lines connect points representing averages for depth of 4, 11, 24, and 29 m. The unbroken lines connect the mid-points in the broken lines and suggest a lowering of efficiency with increasing depth.

II. QUALITATIVE AND QUANTITATIVE DATA

All specimens collected in the area and the abundance of each at various levels are indicated in Tables 17, 18, and 19 below. Unfortunately the worms were lost before identification was complete. The available data pertaining to them is presented merely for its quantitative value.

Fishes move rapidly as compared with most other animals and readily escape from collecting devices. Furthermore, differences in habits and reactions of various species tend to make any collection equipment selective. The area covered by the dredge and trawl hauls ranged from 180 to 230 m². The average was about 200 m². The number of fishes of each species taken in each haul was reduced to a number that might have been caught in a 200 m² haul if the apparatus had taken fishes at the same rate. This made only a small change in most of the figures. To avoid the resulting fractions they

TABLE 17. Showing dominants and slow-moving influents of the area of study (Station 51) together with taxonomically related forms.

The figures indicate the estimated numbers of individuals per 10m². ‡ marked items are estimates from dredge and trawl hauls. Column 1 represents a depth range of 2-6 m and includes dredge haul *a*, trawl haul 2 and bottom sample substation 1 (Fig. 14). Column 2 covers a depth range of 8-12 m. Data included are from trawl haul 1, dredge haul *l* and bottom sampler substations 3, 4, 5, and 6. Column 3 covers bottom sampler substation 7 and dredge hauls *c*, *d*, *e*, and *n*. The depth range is 11-20 m. Column 4 represents dredge hauls *o* and *p* and bottom sampler substations 8 and 9. The depth range is 21-26 m. Column 5 includes bottom sampler substations 12 and 13 and dredge hauls *g* and *h*. The depth range is 21-33 m. Column 6 represents all depths greater than 24 m. Bottom sampler substations 14 and 15 and dredge hauls *i* and *j* are included. Species considered dominants and slow moving influents are indicated by †.

Species	Column					
	1	2	3	4	5	6
STARFISHES						
†*Orthasterias columbiana* Ver.	....	....	....	....	6	1
Ophiopholis aculeata (Linn.) Gray (brittle star)	....	....	....	....	....	12
Evasterias acanthostoma Ver.	....	....	....	....	....	11
Luidia foliolata Grube (fragile star)	....	....	....	....	....	1
SEA CUCUMBERS						
Cucumaria sp. (white cucumber)	20	90	2	....	....	....
†*Stichopus californicus* Ed. (large red cucumber)	....	....	....	....	6	28
SEA URCHINS						
†*Strongylocentrotus drobachiensis* Müller (green urchin)	100	22	36	52	26	22
†*Strongylocentrotus franciscanus* A. Ag. (red urchin)	....	....	....	4	12	4
MUSSELS, CLAMS, PECTONS, ROCK OYSTERS						
Macoma sp.	12	....	....	....	....	....
Cardium corbis Martyn (cockle)	18	50	10	....	....	....
Modiolus modiolus Linn.		20	....	....	10	10
Paphia staminea Conrad	8	40	....	30	....	....
Cardium californiense Desh.	2	80	38	10	30	30
Marcia subdiaphana Carpenter (thin shelled clam)	9	40	....	80	10	66
Venericardia ventricosa Gould	30	1‡	....	....	20	130
Nucula castrensis Hinds, (camp nutshell)	2	....	....	....	....	450
Macoma nasuta Conrad, (bent nose clam)	10	80	....	....	40	....
Macoma secta Conrad	....	13‡	....	....	....	....
Macoma yoldiformis Carp.	....	20	....	....	....	....
Yoldia scissurata Dall.	....	168‡	20	110	10	960
Yoldia ensifera Dall.	....	44‡	30	10	....	83
Solen sicarius Gould	....	10	....	10	10	30
Pandora filosa Carp. (asymmetrical bivalve)	....	20	....	....	....	30
Phacoides tenuisculptus Carp.	....	....	....	100	....	....
Yoldia myalis Couth.	....	....	....	....	....	60
†*Pecten hindsii* Carp. (scallop)	2‡	7‡	....	21‡	....	22‡
†*Pecten hericius* Gould (scallop)	....	4‡	62‡	59‡	28‡	60
Pododesmus macroschisma Desh.	20	13	....	10	10	20

TABLE 17 (Continued)

Species	Column					
	1	2	3	4	5	6
BARNACLES						
†*Balanus pugetensis* Pil.	360	88‡	....	....	....	22‡
Balanus sp.	....	11‡	....	....	....	....
†*Balanus nubilis* Dar.	....	4‡	....	....	....	20‡
†*Balanus rostratus* Hoek.	....	....	....	248‡	10	....
TUNICATES						
Pyura haustor (Stim.)	2‡	10	....	....	....	....
Styela gibbsii (Stim.)	2‡	....	....	....	10	2‡
Boltenia villosa (Stim.)	....	....	....	38‡	6‡	1‡
Corella willmeriana Herd.	....	....	....	11‡	....	6‡
SNAILS, LIMPETS, CHITONS, NUDIBRANCHS, SLIPPER SHELLS						
Nitidella gouldii Carp.	....	30	....	40	....	30
Margarites lirulatus Carp.	360	80	....	20	....	....
Chrysodomus tabulatus Baird	94‡	80	....	23‡	....	22‡
Lacuna divaricata Fab.	440	147	....	....	....	100
Margarites pupillus Gould	1460	122	....	22‡	....	10
Polinices pallida Brod & Sow.	4‡	570	....	34‡	60	30
†*Trichotropis cancellata* Hind.	....	130	....	....	....	....
Calliostoma variegatum Carp.	....	30	....	12‡	30	....
Calliostoma annulatum Martyn	....	....	....	3	....	....
Searlesia dira Reeve	4	17	....	....	63	4
Acmaea mitra Esch.	12	39	....	....	....	....
Acmaea asmi Mid.	....	21	....	....	....	....
Mopalia ciliata Sow.	2	....	....	....	....	....
Lepidochitona lineata Wood., (painted chiton)	5	24	....	....	....	....
Melibe leonina Gould	3	....	....	....	....	....
†*Calyptraea fastigiata* Gould, (Chinese hat)	24	30	17	30	76	160
†*Crepidula nivea* C. B. Adams	2	61	8	....	10	22
WORMS						
Nemerteans	40	20	....	....	....	....
Sternaspis fossor Stimp.	....	90	....	....	....	30
Nereidae, Nephthydidae, etc.	48	1120	130	300	100	138
Other Errantia	14	70	....	10	10	....
Sedentaria	16	360	60	270	30	23
Turbellaria	....	10	10	70	....	....
TOTAL (worms only)	118	1670	200	650	140	191

were multiplied by 10 and hence represent the fishes that might have been taken on 2000 m^2 under similar conditions if caught at the same rate.

III. MAJOR COMMUNITIES

(1) MACOMA-PAPHIA BIOME

The following dominants and influents which are known to characterize the Macoma-Paphia biome (clam beach community) at or near the low tide line were found:

Macoma nasuta Conrad, bent-nosed clam.

Macoma secta Conrad, clam.

TABLE 18. Invertebrate influents found in the area—Station 51.
For interpretation of column headings see Table 17.

Species	Column 1	2	3	4	5	6
SHRIMPS						
Pandalus danae Stim.	1‡	147‡	1049‡	67‡	129‡	67
Spirontocaris prionota (Stim.)	....	4‡	10	....	....	6
Pandalus stenolepis Rath.	....	238‡	359‡	188‡	1248‡	55‡
Crago alaskensis (Loċk.)	....	242‡	414‡	315‡	621‡	65‡
Paracrangon echinata Dana	....	2‡	68‡	36‡	229‡	150‡
Spirontocaris groenlandica (Fab.)	....	2‡	34‡	63‡	2	105‡
Spirontocaris tridens Rath.	....	7‡	32‡	2‡	9‡	14‡
Spirontocaris suckleyi (Stim.)	....	14‡	132‡	521‡	....	....
Spirontocaris kincaidi Rath.	....	....	362‡	33‡	....	....
Pandalus sp.	....	....	4‡	....	75‡	2‡
Pandalus hypsinotus Brandt	....	....	452‡	332‡	9‡	102‡
Crago munita (Dana)	....	....	....	....	12‡	7‡
CRABS						
Pagurus granosimanus (Stim.) hermit crab	20	....	....	....	....	....
Telmessus cheiragonus (Til.), Rath., hermit crab	100	....	....	....	....	....
Pagurus beringanus (Bened.), hermit crab	20	3‡	....	....	....	....
Cancer productus Rand, edible crab	100	100	....	....	....	....
Oregonia gracilis Dana, decorator crab	21‡	67‡	20	....	42‡	....
Pagurus tenuimanus (Dana)	2‡	4‡	....	....	8‡	11‡
Pagurus alaskensis Bened., hermit crab	10	2‡	....	10	18‡	14‡
†*Cancer oregonensis* (Dana) Rath., hairy cancer crab	1‡	53‡	40‡	102‡	7‡	15‡
Pugettia gracilis Dana, graceful crab	20	14‡	5‡	15‡	7‡	44‡
Epialtus productus Rand., kelp crab	100	66‡	5‡	....	2‡	14‡
Pagurus hirsutiusculus (Dana), hermit crab	110	5‡	10	....	....	6‡
†*Hyas lyratus* Dana	....	69‡	212‡	10	20	57
Paguristes turgidus (Stimp.), hermit crab	....	8‡	6‡	....	....	2‡
Pagurus dalli (Bened.), hermit crab	....	121‡	15‡	....	....	....
Pagurus splendescens Owen, hermit crab	....	....	8‡	....	1‡	2‡
Pagurus kennerlyi (Stimp.), hermit crab	....	....	....	143‡	....	2‡
Pagurus ochotensis Brandt, hermit crab	....	....	....	....	....	2‡
AMPHIPODS AND ISOPODS						
Caprella sp.	240	....	....	....	....	....
Idotea resecata Stim.	154‡	....	....	....	....	....
Idotea wosnesenskii Brandt	38‡	....	....	....	....	....

‡Values calculated from catches of dredge or trawl.

Macoma sp., clam.

Cardium corbis Martyn, cockle.

Paphia staminea Conrad, little neck clam.

Pagurus granosimanus (Stim.), hermit crab.

Pagurus beringanus (Bened.), hermit crab.

Telmessus cheiragonus (Til.), hermit crab.

Cancer productus Rand., cancer crab.

The distribution and abundance of species characteristic of this community emphasizes the fact that it is essentially *sub-tidal* although it survives in the soil water of exposed beaches up to a meter or more above mean low tide. Its lower level is shown by our data to lie at a depth of approximately ten

TABLE 19. Showing vertebrate influents found in the region.

Values indicate estimates per 2000 m² based on dredge and trawl catches. Column 1 represents depths of 2-6 m; column 2, depths of 8-12 m; column 3, depths of 11-20 m; column 4, depths of 21-26 m; column 5, depths of 21-33 m; column 6, depths of 24-34 m.

Species	Column					
	1	2	3	4	5	6
INFLUENT FISHES						
Rhinogobiops nicholsii (Bean), small fish		17				
Hippoglossoides elassodon J. &. G., flounder		8				
Lyconectes aleutensis Gilbert, red devil		8				
Pholis ornatus (Girard), chameleon blenny		8				
**Rhamphocottus richardsoni*, Günther, grunt fish		8				
Pleuronichthys coenosus Gir., flounder		8	18			
Hemilepidotus hemilepidotus (Til.), red sculpin			18			
**Myoxocephalus polyacanthocephalus* (Pal.), great sculpin			18			
Eumicrotremus orbis (Gunther), warty lump sucker			18			8
**Icelinus borealis* Gil., northern sculpin			18			26
Chitonotus pugetensis (Steindachner), rough backed sculpin			35	17		7
Lepidopsetta bilineata (Ayres), rock flounder			89	53	26	8
Nautichthys oculofasciatus (Gir.), sailor fish				18		
Hypsagonus quadricornis (Cuv. & Val.), sea poacher				2		
Dasycottus setiger Bean, woolly sculpin				8		
Blepsias cirrhosus (Pallas), silver spot sculpin				8		26
Odontopyxis trispinosus Lock., pitted sea poacher				18		35
Careliparis dennyi (Jor. and Starks), sea snail					8	
Xeneretmus triacanthus (Gil.), sea poacher						35

*Forms considered influents by Shelford (see p. 282.)

meters below mean low tide. Maximum abundance of animals is sub-tidal. The ecotone between the Macoma-Paphia and the Strongylocentrotus-Argobuccinum biomes covers depth ranges from approximately three to ten meters, measured from mean low tide.

(2) STRONGYLOCENTROTUS-ARGOBUCCINUM BIOME

The Strongylocentrotus-Argobuccinum biome (a community of large echinoderms and mollusks) presented a modified composition or faciation within the area studied. All dominants and slow-moving influents listed by Shelford, p. 281, as usually present throughout this biome were encountered with exception of the following:

Argobuccinum oregonensis Red., snail.
Calliostoma costatum Martyn, snail.
Psolus chitonoides Clark, sessile cucumber.
Amphissa columbiana Dall., snail.
Cucumaria miniata Brandt, sea cucumber.

In this particular year Argobuccinum was at a low point in its abundance but it is common on such bottoms in years of abundance. From the usual distribution of Calliostoma and Amphissa there appears to be no reason for absence except a scarcity which caused them to escape collection. Psolus and *C. miniata,* however, are associated with rocks which are wanting in the area.

a. Cardium-Solen faciation of the Strongylocentrotus-Pugettia association (characterized by *S. franciscanus* and *P. gracilis*)

The place of the four Strongylocentrotus-Argobuccinum dominants noted above was taken by such forms as *Cardium californiense* Carp., *Yoldia scissurata* Dall, *Solen sicarius* Gould and *Venericardia ventricosa* Gould. Cardium is most uniformly distributed and is easily recognized. It is nearly always found on muddy bottom within the biome. Solen is less abundant, but is a characteristic form in the area. Hence, these species are given recognition in the naming of the faciation.

b. Algal faciations

Both types of algae which were used by Shelford, Part 1, p. ???, to designate faciations occur in the area, but their distribution was such that differentiation between the animal populations associated with them was impossible. Brown and red algae found in or near mid-channel were:

Brown Algae	*Red Algae*
Laminaria sp.	Callophyllis sp.
Alaria sp.	Nitophyllum sp.
Agarum sp.	Gracilaria sp.
Cymatheria sp.	
Desmerestia sp.	
Monostroma sp.	

(3) PANDORA-YOLDIA BIOME (ABSENT)

Although representatives of the Pandora-Yoldia biome might have been expected on a mud bottom such as was dealt with in this study, the four dominants and slow-moving influents (Shelford, see p. 283) listed below were not encountered:

Scalibregma inflatum Rathke.
Yoldia limatula Say.
Pycnopodia helianthoides (Br.).
Cucumaria populifera (Stimp.).

Three of the remaining four were far less numerous than Shelford or Weese (cf. Table 13, p. 316) found them at corresponding depths during the same year, as shown in Table 20 below.

TABLE 20. Showing abundance of certain Pandora-Yoldia dominants within the area as compared with their abundance within the biome in 1926.

Species	Number per 10 m^2 on plot here studied	Number per 10 m^2 from Shelford's data for corresponding depths see Table 1, 271 also p. 269
Marcia subiaphana Carp.	9–80	16
Yoldia ensifera Dall	10–93	541 {Y. ensifera and Y. limatula
Sternaspis fossor Stim.	30–90	200
Pandora filosa Carp.	20–30	350

Marcia subdiaphana Carp. is the only one of these species with a wide distribution over the area. None of the species which Shelford (see p. 265) considers characteristic of the Pandora-Yoldia biome were collected. This community is not regarded as present in the area of study.

IV. Conclusions

1. The Strongylocentrotus-Argobuccinum biome, large echinoderm-mollusk community, covers muddy bottoms within its climatic area. Certain species are missing, however, and forms which are characteristic of such areas within the biome take their places.

2. Only a few species characteristic of the Pandora-Yoldia biome, small bivalve worm community, occur in isolated mud bottom regions within the climatic area of the Strongylocentrotus-Argobuccinum biome. They are found in reduced numbers there as compared with the biome in which they are dominants.

3. The lower limit of the Macoma-Paphia biome, clam beach community, is established at a depth of approximately ten meters.

4. The ecotone or transition which involves the Strongylocentrotus-Argobuccinum and Macoma-Paphia biomes covers a depth range of 3 to 10 m, measured from mean low tide.

5. In general terms the study when compared with the work of Shelford, Part I, p. 290, shows that the circulation and general condition of the water, together with correlated factors such as amount of plankton, amount of detritus, decomposition products, and oxygen, control the communities present on bottoms classified as mud to a greater extent than the observable character of the mud itself. The organisms constituting the prevalents or most abundant constituents of the community are better indicators of conditions than physical instruments. The use of instruments and measurements should not be neglected, however.

ACKNOWLEDGMENTS AND BIBLIOGRAPHY

The writers are all greatly indebted to Dr. T. C. Frye, Director of the Puget Sound Biological Station, for support during the progress of investigations. They are especially appreciative of the use of the station boat and other equipment and for the special expenditures which he made. At various times during the several years which the investigations of Shelford were being carried on his colleagues supplied important pieces of information without which the paper would be incomplete at several points. Professor Trevor Kincaid, University of Washington, Dr. Hilda Rosene and Dr. Leona Sunquist of the Bellingham State Normal School, assisted with the details of the community map near the mainland. Dr. Rosene made two or three special trips to work shore condition around Bellingham Bay. Mrs. Ida S. Oldroyd,

Stanford University Museum; Mr. J. C. Queen, High School, Marshfield, Oregon; Mr. R. S. Denman, Junior College, Long Beach, Cal.; Mr. E. D. Towler, High School, La Grande, Oregon, rendered especially important service making identifications in the field and in supplying notes.

In connection with the work of Weese sincere thanks are due to the following persons without whom this section could not have been written: Dr. E. Berkeley of the Pacific Biological Station, Nanaimo, B. C., who very kindly determined the exceedingly large number of annelids collected in the quantitative work of Weese, many of which were imperfectly preserved; Dr. Paul Bartsch of the U. S. National Museum, who named many of the molluscs; Prof. James A. Macnab, of Linfield College, McMinnville, Oregon, who assisted in the collection and preservation of the animals and in the preparation of a preliminary paper in collaboration with Weese.

In connection with the work of MacLean thanks are due to Mr. Lee H. Townsend who worked with her during the entire period. Rice's work was extended by Miss Elsa Thorsteinson to whom thanks are due for the samples and data from Point Roberts, Washington. Rasmussen is indebted to Dr. T. Wayland Vaughn of the Scripps Institution of the University of California at La Jolla, for many courtesies.

The writers of Part II are indebted to Professor V. E. Shelford for the suggestion of the problem and for aid and encouragement as the work progressed. Mr. P. H. Simer of the University of Illinois, College of Medicine, and Mr. L. D. Van Tilborg of the University of Washington lent valuable assistance in the collection of data in the field. Miss H. Lane of the Omaha (Nebraska) Central High School supplied data collected by her while engaged in a study upon eel grass.

The following supplied various pieces of important information read, and criticized the manuscript, etc.: Dr. J. E. Guberlet, University of Washington; Dr. L. P. Schultz, University of Washington; Dr. F. E. Clements of the Carnegie Institution, Mr. J. C. Queen, Miss Lois F. Shelford, and Mr. R. W. Pillsbury. The contributions of Dr. H. Gran, Mr. J. C. Cross, Mr. S. W. Howe, Miss Clara Kelly and Mr. H. C. Markus, also, the aid given by Dr. D. H. Thompson in designing equipment, are stated at appropriate points in the text.

Identifications of a limited number of specimens are gratefully acknowledged as follows: Fishes—Dr. L. P. Shultz, Dr. E. V. Smith, and Professor Trevor Kincaid; Tunicates—Dr. Willard G. Van Name; Mollusca—Dr. Paul Bartsch and Mrs. Ida S. Oldroyd; Crabs and Shrimps—Dr. W. L. Schmitt, Miss Belle Stevens, and Mr. J. C. Queen; Isopods—Mr. J. O. Maloney; Amphipods and miscellaneous invertebrates—Mr. Clarence R. Shoemaker; Barnacles—Dr. H. A. Pilsbry; Annelids—Dr. A. L. Treadwell and Dr. E. Berkeley; Starfishes—Dr. H. L. Clark and Dr. Austin H. Clark; Nemerteans—Dr. W. R. Coe.

BIBLIOGRAPHY

Allee, W. C. 1923. Studies in marine ecology: I. The distribution of common littoral invertebrates of the Woods Hole region. II. Some physical factors related to the distribution of littoral invertebrates. Biol. Bull. **44:** 167-191; 205-253.

Allen, W. E. 1921. Problems of floral dominance in the open sea. Ecology **2:** 26-31.

1926a. Remarks on surface distribution of marine plankton diatoms in the East Pacific. Science **63:** 96-97.

1926b. Investigations on phyto-plankton in the Pacific Ocean. Proc. 3rd Pan-Pac. Cong., Tokyo 250-263.

1929. Ocean plankton and plankton problems. Sci. Monthly **28:** 232-238.

1932. Problems of Flotation and deposition of marine plankton diatoms. Trans. Am. Micr. Soc. **51:** 1-7.

Andrews, Florence B. 1925. Resistance of marine animals of different ages. Pub. Puget Sd. Biol. Sta. **3:** 361-363.

Andrews, Harry. 1925. Animals living on kelp. Pub. Puget Sd. Biol. Sta. **5:** 25-27.

Apellof, A. 1912. Invertebrate bottom fauna of the Norwegian Sea and North Atlantic. The Depths of the Ocean. chp. **8:** 457-560. London.

Ashworth, V. H. 1901. The anatomy of Scalibregma inflatum, Rathke. Quart. Jour. Micr. Sci. **45:** 237-310.

Atkins, W. R. G. 1922. The hydrogen ion concentration of sea water in its biological relations. Jour. Mar. Biol. Assoc. **12:** 717-771.

Atkins, W. R. G. and Poole, H. H. 1930. The photo-chemical and photo-electric measurement of submarine illumination. Jour. Mar. Biol. Assoc. **16:** 509-514.

Beauchamp, P. de 1923. Etudes de bionomie intercotidale. Les Iles de Re et d'Yeu. Arch de Zool. Exper. et Gen. **61:** 455-520.

Bigelow, Henry B. 1930. A developing viewpoint in oceanography. Science **71:** 84-89.

Blegvad, H. 1914. Food and conditions of nourishment among the communities of invertebrate animals found on or in the sea bottom in Danish waters. Rept. Dan. Biol. Sta. **22:** 41-78.

1916. On the food of fishes in the Danish waters within the Skaw. Rept. Dan. Biol. Sta. **24:** 17-72.

1922. On the biology of some Danish Gammarids and Mysids (Gammarus locusta, Mysis flexuosa, M. neglecta, M. inermis). Rept. Dan. Biol. Sta. **28:** 1-103.

1923. Methoden der Untersuchung der Bodenfauna des Meerwassers. Emil Abderhalden's Handbuch der biologischen Arbeitsmethoden. Teil **5, 9:** 311-330.

1925. Continued studies on the quantity of fish-food in the sea bottom. Rept. Dan. Biol. Sta. **31:** 27-56.

1927. On the annual fluctuations in the age-composition of the stock of plaice. Rept. Dan. Biol. Sta. **33:** 25-42.

1930. Quantitative investigations of bottom invertebrates in the Kattegat with special reference to the plaice food. Rept. Dan. Biol. Sta. **36:** 3-55.

Bovard, J. F. and Osterud, H. L. 1918. A partial list of animals yielding embryological material at the Puget Sound Biological Station. Pub. Puget Sd. Biol. Sta. **2:** 127-137.

Brandt, Karl. 1896. Das Vordringen mariner Thiere in den Kaiser Wilhelm-Canal, Zool. Jahrb. Abt. f. Syst. Geog. u. Biol. d. Thiere **9:** 387-408.

Bruce, J. R. 1928. Physical factors on the sandy beach. Part I. Tidal, climatic and edaphic. Part II. Chemical changes—Carbon dioxide concentration and sulphides. Jour. Mar. Biol. Assoc. (part I) **15:** 535-552; (part II) 553-566.

Bush, Mildred. 1921. Revised key to the echinoderms of Friday Harbor. Pub. Puget Sd. Biol. Sta. **3:** 65-78.

Cameron, A. T. and Mounce, Irene. 1922. Some physical and chemical factors influencing the distribution of marine flora and fauna in the Straight of Georgia and adjacent waters. With a note on the oxygen content of these waters, by C. J. Berkeley. Cont. Can. Biol. n. s. **1:** 39-72.

Carter, N. M., Mobery, E. G., Skoysberg, Taye and Thompson, T. G. 1934. A5.26—The Reporting of Data in Oceanographical Chemistry. Fifth Pacific Sci. Cong. Victoria and Vancouver. Pp. 2123-2127.

Campbell, Mildred H. 1929a. A preliminary quantitative study of the zooplankton in the Strait of Georgia. Trans. Roy. Soc. Can. Ser. 3 Sec. 5 **23:** 1-27.

1929b. Some free-swimming copepods of the Vancouver Island region. Trans. Roy. Soc. Can. Ser. 3 Sect. 5 **23:** 303-332.

1930. Some free-swimming copepods of the Vancouver Island region, II. Trans. Roy. Soc. Can. Ser. 3 Sect. 5 **24:** 177-184.

Clements, F. E. 1905. Research methods in ecology. Lincoln, Neb.

1920. Plant indicators. Carnegie Inst. of Washington, Pub. No. 290.

Colton, H. S. 1916. On some varieties of Thais lapillus in the Mount Desert section, a study of individual ecology. Proc. Acad. Nat. Sci. Philadlephia, **68:** 440-454.

Dall, William Healey. 1920. Annotated list of the recent Brachiopoda in the collection of the United States National Museum, with description of thirty-three new forms. Proc. U. S. Nat. Mus. **57:** 261-377.

1921. Summary of the marine shellbearing mollusks of the northwest coast of America, from San Diego, California, to the Polar Sea, mostly contained in the collection of the United States National Museum. U. S. Nat. Mus. Bull. **112:** 1-217.

Daugherty, Anna M. and Altman, L. C. 1925. Influence of hydrogen ion concentration, salinity and oxygen upon the rheotaxis of some marine fishes. Pub. Puget Sd. Biol. Sta. **3:** 365-368.

Davenport, C. B. 1903. The animal ecology of the Cold Spring sand spit, with remarks on the theory of adaptation. Decennial Pub., Univ. Chicago **10:** 157-176.

Davis, F. M. 1923. Quantitative studies on the fauna of the sea bottom. No. 1. Preliminary investigation of the Dogger Bank. Fishery Investigations Series II **6:** 1-54.

1925. Quantitative studies on the fauna of the sea bottom. No. 2. Results of the investigations in the southern North Sea, 1921-24. Ministry of Agriculture and Fisheries. Fishery Investigations Series II **8:** 1-50.

Drew, Gilman A. 1899. The Anatomy, Habits, and Embryology of Yoldia limatula Day. Mem. from the Biol. Lab. J. Hopkins Univ. No. 3, **4:** 1-37.

Eddy, Samuel. 1925. The distribution of marine protozoa in the Friday Harbor waters (San Juan Channel, Washington Sound). Trans. Am. Micro. Soc. **44:** 97-108.

Edmondson, C. H. 1920. Edible mollusca of the Oregon coast. Occ. papers, Bishop Mus. Honolulu. **7:** 179-201.

Esterly, C. O 1926. Investigations of zooplankton at the Scripps Institute of Oceanography. Proc. 3rd Pan-Pac. Sci. Cong., Tokyo 264-282.

Ford, E. 1923. Animal communities of the level sea-bottom in the waters adjacent to Plymouth. Jour. Mar. Biol. Assoc. **13:** 164-224.

Fraser, C. McLean and Smith, Gertrude M. 1928a. Notes on the ecology of the little neck clam, Paphia staminea Conrad. Trans. Roy. Soc. Can. Ser. 3, Sect. 5 **22:** 249-270.

1928b. Notes on the ecology of the butter clam, Saxidomus giganteus Deshayes. Trans. Roy. Soc. Can. Ser. 3 **22**: 271-286.

Gail, Floyd W. 1922. Photosynthesis in some of the red and brown Algae as related to depth and light. Pub. Puget Sd. Biol. Sta. **3**: 177-193.

Gamble, F. W. 1910. The relation between light and pigment formation in Crenilabrus and Hippolyte. Quart. Jour. Micro. Sci. **55**: 541-584.

Gardner, Nathaniel L. 1922. The genus Fucus on the Pacific Coast of North America. U. of Cal. Pub. Bot. **10**: 1-180.

Gersbacher, W. H. and Denison, Maggie. 1930. Experiments with animals in tide pools. Pub. Puget Sd. Biol. Sta. **7**: 209-215.

Gislen, T. 1930. Epibioses of the Gullmar Fjord: I. Geomorphology and Hydrography. II. Marine Sociology. Kristinebergs Zoologiska Station 1877-1927, no. 3, pp. 1-123; no. 4, pp. 1-380.

Gran, H. H. 1912. Pelagic plant life. The Depths of the Ocean. Chap. **6**: 307-386. London.

1928. The conditions of life for plankton in the coastal waters of northern Europe. Cons. Perm. pour l'Explor. de la Mer. Rapp. et Proc.-verb. Reun. (Rapport Jubilaire) **47**: 196-204.

1931. On the conditions for the production of plankton in the sea. Con. Perm. Internat. Pour Expl. de la Mere Rapp. et Proc.-verb. Reun. **75**: 37-46.

Gran, H. H. and Thompson, T. G. 1930. The diatoms and the physical and chemical conditions of the sea water of the San Juan Archipelago. Pub. Puget Sd. Biol. Sta. **7**: 169-204.

Hall, Ada R. 1918. Some experiments on the resistance of sea-urchin eggs to sulfurous acid. Pub. Puget Sd. Biol. Sta. **2**: 113-119.

Hedley, Charles. 1915. An ecological sketch of the Sydney beaches. Presidential address, 1915: Jour. & Proc. Roy. Soc. N. S. Wales **49**: 15-77.

Hubbs, Carl L. 1928. A check-list of the marine fishes of Oregon and Washington. Jour. Pan-Pac. Res. Inst. **3** : 9-16.

Humphrey, R. R. and Macey, R. W. 1930. Observations on some of the probable factors controlling the size of certain tide pool snails. Pub. Puget Sd. Biol. Sta. **7**: 205-208.

Hunt, O. D. 1925. The food of the bottom fauna of the Plymouth fishing grounds. Jour. Mar. Biol. Assoc. **13**: 560-599.

Huntsman, A. G. 1918. The vertical distribution of certain intertidal animals. Trans. Roy. Soc. Can. Ser. 3. Sect. 4, **12**: 53-60.

1920. Climates of our Atlantic waters. Proc. Am. Fish. Soc. **50**: 326-333.

1924. Limiting factors for marine animals (1, 2, 3). Cont. to Can. Biol. **2**: 83-88, 91-94, 97-114 (No. 3 with M. D. Sparks).

Hutchinson, A. H. 1928. A biohydrographical investigation of the sea adjacent to the Fraser River mouth. Paper II. Factors affecting the distribution of phytoplankton. Trans. Roy. Soc. Can. Ser. 3, Sec. 5 **22**: 293-309.

Hutchinson, A. H., Lucas, C. C., and McPhail, M. 1929. Seasonal variations in the chemical and physical properties of the waters of the Strait of Georgia in relation to phytoplankton. Trans. Roy. Soc. Can. Ser. 3, Sec. 5, **23**: 177-183.

Jensen, P. Boysen. 1914. Studies concerning the organic matter of the sea bottom. Rept. Dan. Biol. Sta. **22**: 1-39.

1919. Valuation of the Limfjord. I. Rept. Dan. Biol. Sta. **26**: 1-44.

Johansen, A. C. 1927a. On the fluctuations in the quantity of young fry among plaice and certain other species of fish, and causes of the same. Rept. Dan. Biol. Sta. **33**: 3-16.

1927b. On a spawning place for winter spawning herring in the northern part of the Belt Sea. Rept. Dan. Biol. Sta. **33:** 17-24.

Johnson, Herbert Parlin. 1901. The Polychaeta of the Puget Sound region. Proc. Boston Soc. Nat. Hist. **29:** 381-437.

Johnson, Myrtle E. and Snook, Harry J. 1927. Seashore animals of the Pacific Coast. New York.

Johnson, M. W. and Thompson, T. G. 1929. The sea water at the Puget Sound Biological Station from September 1927 to September 1928. Pub. Puget Sd. Biol. Sta. **7:** 119-128.

Kincaid, Trevor. 1919. An annotated list of Puget Sound fishes. State of Washington, Dept. of Fisheries. 51 pp.

Kirsop, Frances Mullis. 1922. Preliminary study of methods of examining the life of the sea bottom. Pub. Puget Sd. Biol. Sta. **3:** 129-139.

Krogh, A. 1931. Dissolved substances as food of aquatic organisms. Con. Perm. Internat. pour Expl. de la Mare. Rapp. et Proc.-verb, Reun. **75:** 7-36.

Lebour, M. V. 1919a. Feeding habits of some young fish. Jour. Mar. Biol. Assoc. **12:** 9-21.

1919b. The food of post-larval fish. No. II (1918). Jour. Mar. Biol. Assoc. **12:** 22-47.

1920. The food of young fish. No. III (1919). Jour. Mar. Biol. Assoc. **12:** 261-324.

1921. The food of young clupeoids. Jour. Mar. Biol. Assoc. **12:** 458-467.

1922. The food of plankton organisms. Jour. Mar. Biol. Assoc. **12:** 644-677.

1923a. The food of plankton organisms. II. Jour. Mar. Biol. Assoc. **12:** 70-92.

1923b. The food of young herring. Jour. Mar. Biol. Assoc. **13:** 325-330.

Lucas, C. C. 1929. Further oceanographic studies of the sea adjacent to the Fraser River mouth. Trans. Roy. Soc. Can. Ser. 3, Sec. 5 **23:** 29-69.

Lucas, C. C. and Hutchinson, A. H. 1927. A bio-hydrographical investigation of the sea adjacent to the Fraser River mouth. Trans. Roy. Soc. Can. Ser. 3, Sec. 5 **21:** 485-520.

Lucas, Verna Z. 1931. Some Ostracoda of the Vancouver Island region. Contrib. Can. Biol., N. S. **6:** 397-416.

Mast, S. O. 1914. Changes in shade, color, and pattern in fishes and their bearing on the problems of adaptation and behavior with especial reference to the flounders Paralichthys and Ancylopsetta. Bull. Bur. Fish. **34:** 173-238.

McMurrich, J. P. 1916. Notes on plankton of British Columbia Coast. Trans. Roy. Soc. Can. Ser. 3 **10:** 75-89.

Molander, A. R. 1927. Animal communities on soft bottom areas in Gullmar fjord. Kristineburge Zoologiska Station 1877-1927. No. 2, pp. 1-90.

Monro, C. C. A. 1933. On a new species of polychaete of the genus Pilargis from Friday Harbor, Washington. Ann. and Mag. Nat. Hist. **11:** 673-675.

Moore, H. B. 1931a. Muds of the Clyde Sea area. III. Chemical and physical conditions; Rate and nature of sedimentation; and fauna. Jour. Mar. Biol. Assoc. **17:** 325-348.

1931b. The specific identification of faecal pellets. *Ibid.*, 359-366.

Miles, Ward R. 1918. Experiments on the behavior of some Puget Sound shore fishes (Blenniidae). Pub. Puget Sd. Biol. Sta. **2:** 79-94.

Mossop, Bessie K. E. 1922. The rate of growth of the sea mussel (Mytilus edulis L.) at St. Andrews, New Brunswick; Digby, Nova Scotia; and in Hudson Bay. Trans. Roy. Can. Inst. **14:** 3-22.

Mounce, Irene. 1922. The effect of marked changes in specific gravity upon the amount of phytoplankton in Departure Bay waters. Cont. to Can. Biol. n.s. **1:** 81-93.

Muenscher, Walter L. C. 1915. A study of the algal associations of San Juan Island. Pub. Puget Sd. Marine Sta. **1:** 59-84.

Murray, John and Hjort, Johan. 1912. The depths of the ocean. London.

Newcombe, C. L. 1935. A study of the community relationships of the sea mussel (Mytilus edulis L.). Ecology **16:** 234-243.

O'Donoghue, Chas. H. 1921. Nudibranchiate Mollusca from the Vancouver Island region. Trans. Roy. Can. Inst. Toronto. **13:** 147-209.

1922. Notes on the nudibranchiate Mollusca from the Vancouver Island region. III. Records of species and distribution. Trans. Roy. Can. Inst. Toronto. **14:** 145-167.

1925a. Notes on certain Bryozoa in the collection of the University of Washington. Pub. Puget Sd. Biol. Sta. **5:** 15-23.

O'Donoghue, Chas. H. and O'Donoghue, Elsie. 1922. Notes on the nudibranchiate Mollusca from the Vancouver Island region. II. The spawn of certain species. Trans. Roy. Can. Inst. **14:** 131-143.

1925. List of Bryozoa from the vicinity of Puget Sound. Pub. Puget Sd. Biol. Sta. **5:** 91-108.

Oldroyd, Ida S. 1924. Marine shells of Puget Sound and vicinity. Pub. Puget Sd. Biol. Sta. **4:** 1-272.

Oliver, W. R. B. 1915. The Mollusca of the Kermadec Islands. Trans. and Proc. N. Z. Inst. **47:** 509-568.

1923. Marine littoral plant and animal communities in New Zealand. Trans. and Proc. N. Z. Inst. **54:** 496-545.

Pearse, A. S. 1913. Observation on the fauna of the rock beaches at Nahant, Mass. Bull. Wis. N. H. Soc. **11:** 8-34.

Perry, Edna M. 1916. Distribution of certain invertebrates on a restricted area of sea bottom. Pub. Puget Sd. Marine Sta. **1:** 175-176.

Petersen, C. John. 1913. Valuation of the sea. II. The animal communities of the sea bottom and their importance for marine zoogeography. Rept. Dan. Biol. Sta. **21:** 1-44 and app. 1-68.

1915a. Appendix of Report **21:** 1-7, Rept. Dan. Biol. Sta. **22:** 89-96.

1915b. On the animal communities of the sea bottom in the Skagerak, the Christiania Fjord and the Danish waters. Rept. Dan. Biol. Sta. **23:** 3-28.

1915c. A preliminary result of the investigations on the valuation of the sea. Rept. Dan. Biol. Sta. **23:** 29-32.

1918. The sea bottom and its production of fish-food. Rept. Dan. Biol. Sta. **25:** 1-62.

Petersen, C. G. John and Jensen, P. Boysen. 1911. Valuation of the sea. I. Animal life of the sea-bottom and its food and quantity. Rept. Dan. Biol. Sta. **20:** 1-79.

Pierron, R. P. and Huang, Y. C. 1926. Animal succession of denuded rocks. Pub. Puget Sd. Biol. Sta. **5:** 149-157.

Phifer, L. D. 1933. Seasonal distribution and occurrence of planktonic diatoms at Friday Harbor, Washington. Univ. Wash. Publ. in Oceanog. **1:** 39-81.

1934. A5.9—Periodicity of diatom growth in San Juan Archipelago. Fifth Pacific Science Congress Victories and Vancouver, B. C. 1933, pp. 2047-2049.

1934. Vertical distribution of diatoms in the Strait of Juan De Fuca. Univ. Wash. Publ. in Oceanog. **1:** 83-96.

1934. Phytoplankton of East Sound, Washington, February to November 1932. Univ. Wash. Bull in Oceanog. **1:** 97-110.

Pilsbry, Henry A. 1916. The sessile barnacles (Cirripedia) contained in the collections of the U. S. National Museum; including a monograph of the American species. U. S. Nat. Mus. Bull. No. 93.

Powers, E. B. 1920. The variation of the condition of sea-water, especially the hydrogen-ion concentration, and its relation to marine organisms. Pub. Puget Sd. Biol. Sta. **2:** 369-385.

1921. Experiments and observations on the behavior of marine fishes toward the H-ion concentration of the sea water in relation to their migratory movements and habitat. Pub. Puget Sd. Biol. Sta. **3:** 1-22.

Powers, E. B. and Hickman, T. A. 1928. The carbon dioxide tensions of the Fraser River and its lower tributaries and of certain tributaries of the Columbia River. Pub. Puget Sd. Biol. Sta. **5:** 373-380.

Powers, E. B. and Logan, G. A. 1925. The alkaline reserve of the blood plasma of the viviparous perch (Cymatogaster aggregatus Gib.) in relation to the carbon dioxide tension, the oxygen tension, and the alkalinity of the sea water. Pub. Puget Sd. Biol. Sta. **3:** 337-360.

Rathbun, Mary J. 1904. Decapod crustaceans of the northwest coast of North America. Harriman Alaska Series, Smiths. Inst. **10:** 1-210.

Rice, Lucile. 1930. Peculiarities in the distribution of barnacles in communities and their probable causes. Pub. Puget Sd. Biol. Sta. **7:** 249-257.

Richardson, Harriet. 1904. Isopod crustaceans of the northwest coast of North America. Harriman Alaska Series, Smiths. Inst. **10:** 211-230.

1909. Isopods collected in the northwest Pacific by the U. S. Bureau of Fisheries Steamer "Albatross" in 1906. Proc. U. S. Nat. Mus. **37:** 75-129.

Russell, F. S. 1928a. The vertical distribution of marine macroplankton. VI. Further observations on diurnal changes. Jour. Mar. Biol. Assoc. **15:** 81-104.

1928b. The vertical distribution of marine macroplankton. VII. Observations on the behaviour of Calanus finmarchicus. Jour. Mar. Biol. Assoc. **15:** 429-454.

1928c. The vertical distribution of marine macroplankton. VIII. Further observations on the diurnal behaviour of the pelagic young of teleostean fishes in the Plymouth area. Jour. Mar. Biol. Assoc. **15:** 829-850.

1930a. The vertical distribution of marine macroplankton. IX. The distribution of the pelagic young of teleostean fishes in the daytime in the Plymouth area. Jour. Mar. Biol. Assoc. **16:** 639-676.

1930b. The seasonal abundance and distribution of the pelagic young of teleostean fishes caught in the ring-trawl in off-shore waters in the Plymouth area. Jour. Mar. Biol. Assoc. **16:** 707-722.

1931a. The vertical distribution of marine macroplankton. X. Notes on the behaviour of Sagitta in the Plymouth area. Jour. Mar. Biol. Assoc. **17:** 391-414.

1931b. The vertical distribution of marine macroplankton. XI. Further observations on diurnal changes. Jour. Mar. Biol. Assoc. **17:** 767-784.

Russell, F. S. and Yonge, C. M. 1928. The seas. London and New York.

Scammon, C. M. 1869. On the cetaceans of the western coast of North America. Proc. Acad. Nat. Sci. Phil. **1869:** 13-63.

1874. The marine mammals of the northwest coast of North America. San Francisco.

Schmitt, Waldo L. 1921. The marine decapod Crustacea of California. U. of Cal. Pub. Zool. **23:** 1-470.

Setchell, William A. and Gardner, N. L. 1903. Algae of Northwestern America. U. of Cal. Pub. Bot. **1:** 165-418.

1919. The marine algae of the Pacific coast of North America. Part I. Myxophyceae. U. of Cal. Pub. Bot. **8**: 1-138.

1920. Part II. Chlorophyceae. U. of Cal. Pub. Bot. **8**: 139-374.

1925. Part III. Melanophyceae. U. of Cal. Pub. Bot. **8**: 383-886.

Shelford, Victor E. 1916. Physiological differences between marine animals from different depths. Pub. Puget Sd. Marine Sta. **1**: 157-174.

1918. The relation of marine fishes to acids with special reference to the Miles acid process of sewage treatment. P. S. Biol. Station Pub. **2**: 97-111.

1929. The penetration of light into Puget Sound waters as measured with gas filled photoelectric cells and ray filters. Pub. Puget Sd. Biol. Sta. **7**: 151-168.

1930. Geographic extent and succession in Pacific North American intertidal (Balanus) communities. Pub. Puget Sd. Biol. Sta. **7**: 217-223.

1931a. Some concepts of bioecology. Ecology **12**: 455-467.

1931b. Basic principles of the classification of communities and the use of terms. Ecology **13**: 105-120.

Shelford, V. E. and Eddy, S. 1929. Methoden zur Untersuchung von Flusslebensgemeinschaften. Handbuch der biologischen Arbeitsmethoden, Abt. 9, Teil **22**: 1525-1549.

Shelford, V. E. and Gail, Floyd W. 1922. A study of light penetration into sea water made with the Kunz photoelectric cell with particular reference to the distribution of plants. Pub. Puget Sd. Biol. Sta. **3**: 141-176.

Shelford, V. E. and Powers, E. B. 1915. An experimental study of the movements of herring and other marine fishes. Biol. Bull. **28**: 315-334.

Shelford, V. E. and Towler, E. D. 1925. Animal communities of San Juan Channel and adjacent areas. Pub. Puget Sd. Biol. Sta. **5**: 31-73.

Smith, Gertrude M. 1928. Food material as a factor in the growth rate of some Pacific clams. Trans. Roy. Soc. Can. Ser. 3, Sec. 5 **22**: 287-291.

Southern, R. 1915. Marine ecology. Proc. Roy. Irish Acad. (Clare Island Survey), Sec. 3, part 67) **31**: 1-110.

Spärck, R. 1929. Preliminary survey of the results of quantitative bottom investigations in Iceland and Farœ waters, 1926-1927. Con. Perm. Internat. pour l'Expl. de la Mer, Rapp. et Proc.-verb, Reun. Scientific report of the northwestern Area Committee. **47**: 1-28 (paged separately).

Starks, E. C. 1911. Results of an ichthyological survey about the San Juan Islands, Washington. Ann. Carn. Mus. **7**: 162-213.

Steggerda, Morris and Essex, Hiram E. 1925. Rock bottom fauna of a restricted area near Friday Harbor, Washington. Pub. Puget Sd. Biol. Sta. **5**: 29-31.

Stephen, A. C. 1930. Studies on the Scottish marine fauna. Additional observations on the fauna of the sandy and muddy areas of the tidal zone. Trans. Roy. Soc. Edin., part II **56**: 80-355.

Stevens, B. A. 1926. Callianassidae from the West Coast of North America. Pub. Puget Sd. Biol. Sta. **6**: 315-369.

Stevens, G. A. 1930. Bottom fauna and the food of fishes. Jour. Mar. Biol. Assoc. **16**: 677-706.

Strong, L. H. 1925. Development of certain Puget Sound hydroids and medusae. Pub. Puget Sd. Biol. Sta. **3**: 383-399.

Sumner, F. B., Osburn, R. C., Cole, L. J., and Davis, B. M. 1911. A biological survey of the waters of Woods Hole and vicinity. Bull. Bur. Fish. U. S. Sect. 1 and 2. **31**: 1-860.

Thompson, T. G. and Houlton, H. G. 1933. Determination of silicon in sea water. Ind. Eng. Chem. Anal. Ed., **5**: 417.

Thompson, T.G., Lang, J. W., and Anderson, Lucile. 1927. The sulfate-chloride ratio of the waters of the North Pacific. Pub. Puget Sd. Biol. Sta. **5:** 277-292.

Thompson, T. G., Miller, R. C., Hitchings, G. H., and Todd, S. P. 1929. Studies of the sea water near the Puget Sound Biological Station during the summer of 1927. Pub. Puget Sd. Biol. Sta. **7:** 65-99.

Thompson, T. G., Johnson, M. W., and Todd, S. P. 1926. The sea water at the Puget Sound Biological Station from September 1921 to September 1927. Pub. Puget Sd. Biol. Sta. **6:** 371-391.

Thompson, T. G. and Robinson, R. J. 1934. A5.22—The sea water of the Puget Sound Region. Proc. of the 5th Pacific Sci. Cong., Victoria and Vancouver, B. C. 1933, pp. 2101-2107.

Thompson, T. G., Thomas, B.D., and Barnes, C. A. 1934. Distribution of dissolved oxygen in the North Pacific Ocean. James Johnstone Memorial Volume, pp. 203-234. Univ. Press of Liverpool.

Towler, E. D. 1930. An analysis of the intertidal barnacle communities of the San Juan archipelago. Pub. Puget Sd. Biol. Sta. **7:** 225-232.

Treadwell, Aaron L. 1914. Polychaetous annelids of the Pacific Coast in the collections of the zoological museum of the University of California. U. of Cal. Pub. Zool. **13:** 175-234.

Vaughan, T. W. 1926a. Report of the chairman of the committee on the chemical and physical oceanography of the Pacific. Proc. 3rd Pan-Pac. Sci. Cong., Tokyo 141-167.

1926b. Researches in oceanography in the western part of the United States, Alaska, and the Hawaiian and Philippine Islands. Proc. 3rd Pan-Pac. Cong., Tokyo 238-246.

1926c. International Coöperation in oceanographic investigations in the Pacific. Proc. 3rd Pan-Pac. Sci. Cong., Tokyo 314-321.

1932. Outstanding problems of the oceanography of the Pacific. Sci. Month. **34:** 128-146.

Weaver, J. E. and Clements, F. E. 1929. Plant Ecology. New York.

Weese, A. O. 1926. Food and digestive processes in Strongylocentrotus drobachiensis. Pub. Puget Sd. Biol. Sta. **5:** 165-177.

Weese, A. O. 1933. The annelids of a marine sere. Proc. Okla. Acad. Sci. **13:** 18-21.

Weese, A. O. and MacNab, J. A. 1930. Seral communities of a muddy sea bottom. Proc. Okla. Acad. Sci. **10:** 26-28.

Weese, A. C. and Townsend, M. T. 1921. Some reactions of the jelly-fish, Aequoria. Pub. Puget Sd. Biol. Sta. **3:** 117-128.

Wells, Wayne W. 1928. Pinnotheridae of Puget Sound. Pub. Puget Sd. Biol. Sta. **6:** 283-314.

Williams, Marvin. 1929. Horizontal upward intensity of light in Puget Sound waters. Pub. Puget Sd. Biol. Sta. **7:** 129-135.

Wilson, Paul T. 1926. A brief study of the succession of clams on a marine terrace. Pub. Puget Sd. Biol. Sta. **5:** 137-148.

Worley, Leonard G. 1930. Correlation between salinity, size and abundance of intertidal barnacles. Pub. Puget Sd. Biol. Sta. **7:** 233-240.

Zenkevitsch, L. A. 1927. Materialien zur quantitativen Untersuchung der Bodenfauna des Barents und des Weissen Meeres (in Russian). Berichte des Wissensch. Meeresinstituts. Pt. 4. **2:** 1-64.

1930. Ueber den neuen Bodensgreifer von Knudsen (in Russian, with German summary). Russischen Hydrobiologischen Zeitschrift. **7:** 201-203.

Zenkewitch, L. 1931. On the aeration of the bottom waters through vertical circulation. Jour. Const. Internat. pour l'Expl. de la Mer. **6:** 402-418.

SOME PRINCIPLES OF COMPETITION AS ILLUSTRATED BY SUDAN GRASS, *HOLCUS SORGHUM SUDANENSIS* (PIPER) HITCH.

By

FERNANDO DE PERALTA
University of Nebraska

CONTENTS

SOME PRINCIPLES OF COMPETITION AS ILLUSTRATED BY SUDAN GRASS, *HOLCUS SORGHUM SUDANENSIS* (PIPER) HITCH.*

INTRODUCTION

No student of field ecology can doubt the fundamental importance of competition either in the development of natural vegetation or in the production of cultivated crops. There is great need, however, of replacing qualitative knowledge of competition by experimental, quantitative data. This is especially true in studies of crop plants where, with few exceptions, only the final results of competition, as expressed by yields, have been determined. Sudan grass was suggested as an excellent plant to use in studying the principles of plant competition. It grows so rapidly that it uses large amounts of water and nutrients and the shade cast is such that competition for light soon becomes an important factor.

The history of the competition concept has been given by Clements, Weaver, and Hanson (1929) in their monograph on competition. This includes a statement of the earliest views; modern experimental studies, including materials furnished by investigators on plant succession; and a special statement of plant competition in forest and cultivated fields. They point out that competition in field and garden differs in two important respects from that in natural communities. It is, in the absence of weeds, between the individuals of one species or variety, and the habitat is controlled in as large a degree as possible in favor of the crop. These writers, by their work in field and garden, have also contributed in a large measure to the knowledge of competition of crop plants begun by Montgomery (1910, 1912), extended by Kiesselbach and coworkers (1918, 1923, 1928, 1933), and furthered by numerous other investigators. Because of their historical analysis, a further summary of the literature at this time is unnecessary.

As understood by the writer, competition is purely a physical process. It is essentially a decrease in the amount of water, nutrients or light available for each individual, and therefore increases with the density of the plant population. With few exceptions, an actual struggle between two plants never occurs.

The writer is under deep obligation to Dr. J. E. Weaver for outlining the problem and for efficient direction throughout the entire course of the work.

SELECTION OF PLOTS

An area of moderately low, level land, on the flood plain of Salt Creek, and two miles north of the Capitol Building in Lincoln, Nebraska, was

* Contribution from the Department of Botany, University of Nebraska, No. 91.

selected for these studies. The field, which had been farmed for only a few years, was originally a part of the Belmont prairie. It was selected because both soil and subsoil contained enough sand to facilitate root excavation; because of the absence of perennial weeds; and, especially, because of the uniformity of the soil. A plot 200 feet long and 75 feet wide was located at the foot of a long slope facing southeastward. It had previously been cropped to sweet corn, the size of the stalks and the yield indicating a fairly high degree of fertility.

Soil

The soil is classified as Wabash silt loam (colluvial phase). It revealed a buried profile as is not infrequently the case in similar soils adjacent to uplands (Weaver, Hougen, and Weldon, 1935). The surface 18 inches consisted of a dark-brown sandy loam. It was darker in color in the first 6 inches, but rather uniform throughout. The second 6 inches was mottled with a considerable quantity of light colored sand which added a grayish tone. The soil was very friable and easily penetrated by roots.

At 18 inches depth there occurred the top of the former surface soil. It was very dark brown or black in color. Its excellent granular structure and apparent high humus content showed conclusively that it was at one time the surface soil. This original "A" horizon contained distinctly more clay than the soil above. It was 14 inches thick.

A gradual transition to the "B" horizon occurred at a depth of 32 inches. Here the soil was yellowish-brown in color, of higher clay content, and less friable than the layer immediately above. It was not so thoroughly penetrated by roots. When moist, it was easily excavated since it contained enough sand to give it a good structure.

The transition to the "C" horizon or massive layer was rather gradual. The massive layer became clearly apparent at about 48 inches. Here the soil was of reddish brown or yellowish brown color and very friable. It contained less clay and more sand and was much more readily removed than the layer above. It was well drained, and occupied by numerous roots. There were some streaks and mottling with iron. No lime concretions were in evidence. The massive layer extended deeply without much change.

The hygroscopic coefficient of the surface 4 inches was 10.6 per cent; that of the 4 to 12 inch depth, 11.1. Those of the second, third, and fourth feet were 11.3, 8.7, and 8.6 per cent respectively. Hygroscopic coefficients of the first three feet of the massive layer were somewhat similar, varying between 8.8 and 9.9 per cent. The surface layer was acid, pH 4.9, and that of the 4 to 12 inch depth slightly less so, pH 5.2. The second, third, and fourth feet gave pH values of 5.9, 6.0, and 6.0, respectively. Acidity decreased with depth, from pH 5.8 in the sixth foot to 6.4 in the eighth.

GENERAL CONDITIONS FOR GROWTH

The mean annual precipitation at Lincoln over a period of 56 years is 27.8 inches. Approximately 79 per cent of this falls as rain during the months of April to September inclusive. Although the rains occur largely as thundershowers with heavy precipitation falling during a short period of time, yet because of the nearly level topography and sandy nature of the soil in the experimental plots, there was no run-off. Periods of drought extending over two or more weeks are common. Average day air temperatures sometimes reach 90°F. but are more usually between 75° and 85°F. Average day humidities vary between 50 and 80 per cent during years of greater rainfall but fall frequently to 40 to 50 per cent during drier years. Wind movement is fairly constant and often high; about 72 per cent of the summer days are entirely clear; and evaporation is high, often averaging 30 cc. daily (Weaver and Himmel, 1931).

The growing season of 1933 was marked by a very dry spring (April and May), although this was preceded by abundant rains in March. Rainfall during June was also below normal; temperatures were extremely high, and the humidity unusually low. Well distributed rains occurred during July, accompanied by moderate temperature and humidity. Drought occurred during the first half of August, resulting in the exhaustion of soil moisture and the ripening of the Sudan grass.

PREPARATION OF SOIL—PLAN OF PLOTS

The cornstalks with the attached coarser roots were removed from the field, which was otherwise free of weeds or other litter. The field was then disked and repeatedly harrowed, thus preparing an excellent seed bed. It was then divided into eight major plots, each 75 feet long and 25 feet wide. These are designated, in accordance with the rate of seeding, normal (N), twice normal (2N), and one-half normal (½N) etc., as shown in Figure 1, where it may be observed that all except the 3N and ¼N plots were in duplicate. Each of the major plots was divided into three smaller ones designated respectively in Figure 1 as A, B, and C. Each subplot A was 25 by 40 feet in extent. The central areas in the plots, each of 100 or 200 square feet, were the portions cut to determine yields. Those in subplots A were cut only after the grain had ripened; those in B and C at approximately fortnightly intervals, the former to a height of 6 inches and the latter to a height of 2 inches.

RATE AND METHOD OF SOWING

The entire field was planted to Sudan grass on May 22, 1933. The normal rate of sowing was 22 pounds per acre (Kiesselbach and Anderson, 1925; Aldous and Zahnley, 1931). The 2N plots received twice this amount of

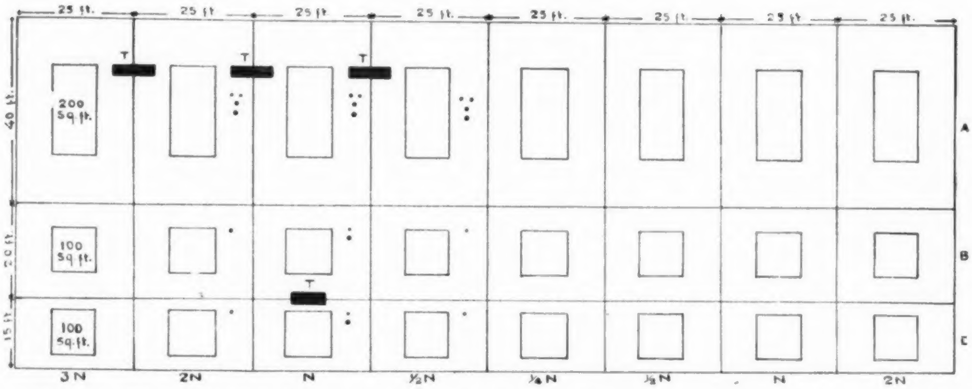

FIG. 1. Plan of experimental plots with subdivisions as described in the text. The trenches excavated in studying roots are indicated by T, and the positions of the insert phytometers by dots.

seed and the other plots the relative amounts designated by their names respectively.

Since repeated experiments indicate that drilling has little advantage over broadcasting, the seeds were sown by the latter method (Hughes and Wilkins, 1926). In order to secure a uniform rate of planting, the lot of seed for each major plot was thoroughly mixed with about 15 pounds of soil. The mixture was then divided into halves. One-half was broadcasted by hand lengthwise of the plot and the other half crosswise. After sowing, the field was harrowed twice. Since the soil was in excellent tilth, this covered the seeds quite uniformly.

METHODS AND PROCEDURE

The rate of growth of the plants under each density of planting was determined by weekly measurements of increase in height of selected plants of average size in each plot. The dry weight of tops was also determined at various intervals. In these determinations 50, and later 25, plants of average size were selected from each plot. Measurements of the dimensions of leaves and area of stems and counts of the number of tillers were made. Dry weight was also determined. The area of the parts above ground was ascertained by means of blue prints and a planimeter. The leaves were cut at the ligule or, if only partly unfolded, where they emerged from the sheath. They were carefully flattened for making the prints. The area of the stems was calculated after measuring the diameter and length. Finally, the plants were cut into pieces of convenient size and dried in an electric oven at 98°C. until they reached a constant weight.

Determinations were made of the relative osmotic pressures of the cell sap of the leaves under different rates of planting. Studies were also made on the anatomical structure of leaves and roots under several different degrees of competition.

Phytometers were used in order to measure directly the water losses during various intervals from unit areas of the plots both under different densities of planting and heights of cutting. They were also used for determining weight and volume of roots and tops. These consisted of containers of three different sizes planted to Sudan grass at the time of seeding the plots. Three had a cross-sectional area of 1 square foot and were 2 feet deep, five had 76 square inches of soil surface when filled and were 2.5 feet deep. Twelve smaller ones, in which the plants were grown for shorter periods, were 54 square inches in area of tops and 1.5 feet deep (Fig. 2). Each container was filled with the soil dug from the hole where it was installed and in such a manner that each six-inch layer of soil occupied the same depth in the con-

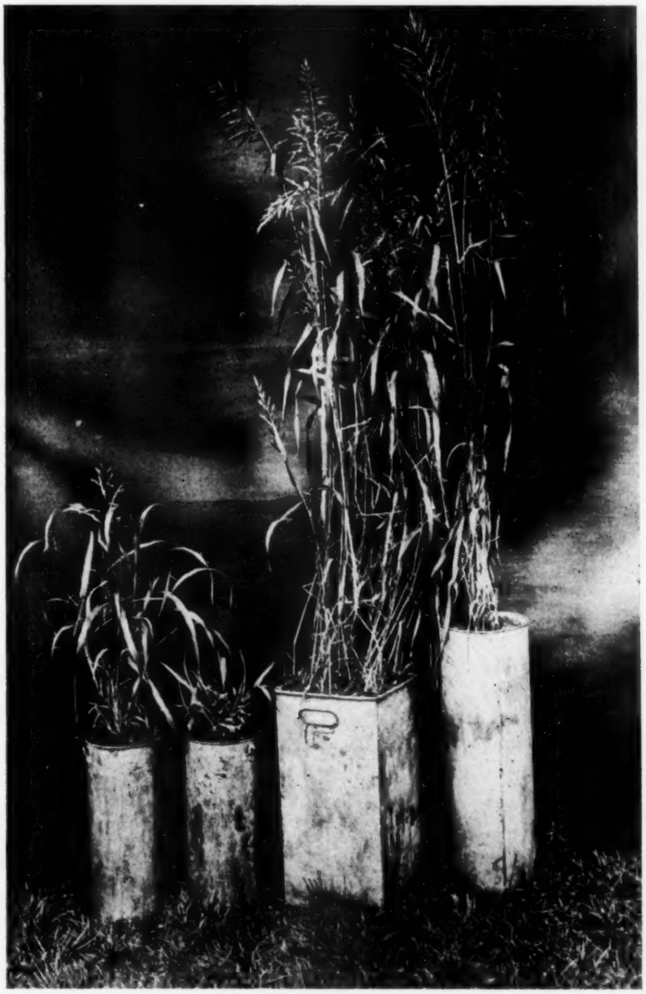

FIG. 2. Types of phytometers used in studies of water loss, and weight and volume of roots under different degrees of competition and clipping. In the large ones on the right, the plants were 6 ft. tall on July 21.

tainer that it had formerly occupied in the field. The tops of the containers were slightly above the soil surface so that they received no run-off water. Each hole was just large enough to receive its container and the container was surrounded by Sudan grass of the regular thickness of planting for that plot. The Sudan grass was sown thickly in the container so as to insure a thick stand and thus permit of thinning to the same density of stand as that of the crop surrounding each container. The locations of the different types of phytometers are shown in Figure 1. Competition was also measured by growing isolated sunflowers in the several plots.

The dry weight and volume of the root systems were determined at several intervals from the plants grown in the containers. This was done because of the difficulty of recovering the entire root system unless enclosed. At the completion of the studies on water loss, the roots were recovered by cutting the container open lengthwise, after placing it in a slanting trough. The soil was washed away with a fine spray of water from a hose and the root systems left almost completely intact. The muddy water was allowed to run through a screen of 2 mm. mesh, upon which the few broken root-ends collected and were recovered. All surface water was removed by pressing the roots repeatedly for a few minutes between blotting paper, and the volume was then determined by immersing them in water contained in a graduated cylinder and ascertaining the volume of the water displaced. This equalled the volume of the roots.

The development of the root system under normal rate of planting was determined at regular intervals by the direct, trench method described by Weaver (1926). At each time of excavation the root systems of several plants, with tops of average size, were exposed and measured. After numerous measurements, a typical root system was selected and drawn to scale. Comparative studies were made on the root development in the thicker and thinner plantings and in the plots that were cut at different heights. Although the same trenches (Fig. 1) were used throughout, they were not only refilled after each excavation but also sufficiently enlarged at the following excavation so that all roots were taken from normal, undisturbed soil.

Soil sampling for water content was done with a Briggs' geotome. Duplicate samples of about 200 grams were secured from the several soil layers to a depth of four feet. Each sample was brought to a constant weight at 110°C. and water content was based on the dry weight of the soil. Soil acidity was determined by the quinhydrone method. Other factor measurements were made as described by Weaver and Clements (1929).

For the sake of clarity, the development of the tops and roots of Sudan grass from seed to maturity, *i.e.*, its life history under the normal rate of planting, will be given first. The effects of competition under different rates of planting will then be discussed. Finally, the behavior of the plants under different heights of cutting will be given.

LIFE HISTORY OF SUDAN GRASS

The large seeds sown on May 22, germinated rapidly in the warm, moist soil, planting having been immediately followed by rain. Numerous shoots appeared above the soil surface after four days.

DEVELOPMENT OF SEEDLINGS

Many small plants were excavated and a representative sample was drawn (Fig. 3A). Although the shoot was only an inch high, the primary root was three inches long. It was about a millimeter in diameter, turgid, white, and had developed no branches.

Three days later the first leaf had attained a length of 2 inches and the second one, although not fully grown, was slightly longer. The spread of the leaves was already 2.5 inches. The primary root was 4.5 inches long, and branch roots of the first order were quite abundant near the surface of the soil. Penetration was nearly vertically downward (Fig. 3B).

Growth continued so rapidly that only four days later, on June 2, a height of 4 inches had been attained. The shoot had 3 leaves, and the fourth was appearing. The longest leaf measured 4 inches. The primary root had extended nearly straight downward to a depth of 9.5 inches. Many branch roots of the first order had developed. Some had extended laterally to a maximum distance of 1.5 inches. A single root system occupied a cylinder of soil 2.5 inches in diameter and 9.5 inches deep (Fig. 3C).

During the following period of 3 days the shoot had unfolded a fourth leaf and the tip of the fifth was over 4 inches long. The roots had made a steady growth. The primary root continued its vertically downward course to a depth of 10.5 inches and long branch roots entended laterally. Short roots of the second order now occurred for the first time. The first root of the secondary root system also appeared on June 5, 14 days after planting. It originated from the lowest node of the shoot. It was 2 mm. thick and well supplied with root hairs.

After three more days of growth, the seedlings were 5.5 inches high; they had 5 or 6 leaves each and a spread of leaves of about 5 inches (Fig. 3E). The first tiller was beginning to develop in the axil of the lowest leaf. The primary root was 13 inches long. Both primary and secondary laterals had made a good growth, and the older portions of the main root had begun to decorticate. The secondary root system had added two new roots, both arising from the lowest node. The oldest was nearly 3 inches long. They penetrated rather vertically downward.

The ability of this crop to withstand high temperatures, low humidities, and severe drought was clearly exhibited during this period. On the afternoon of June 9, for example, the air temperature was 108°F. four feet above the soil surface and 116°F. four inches above the surface. The surface soil

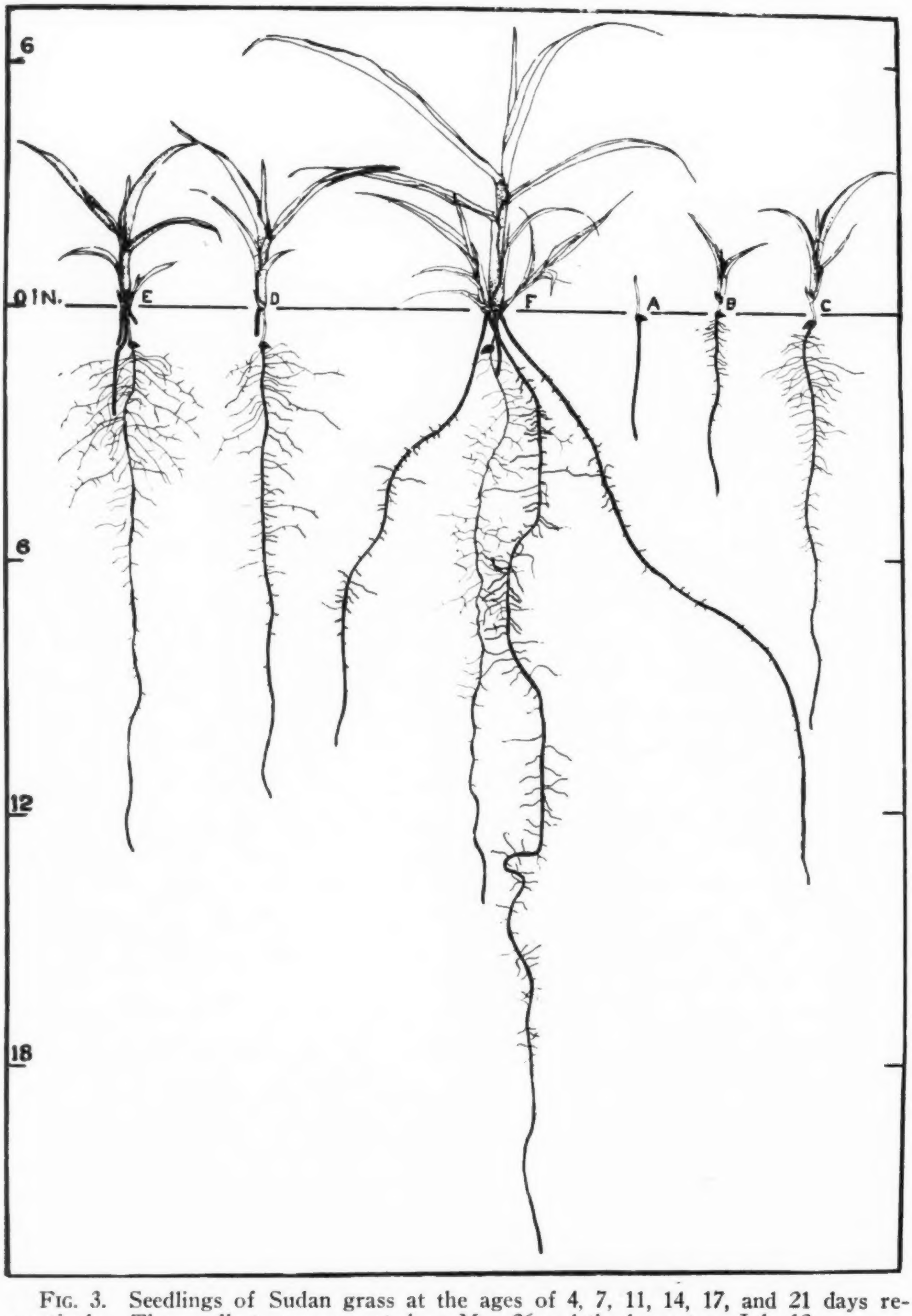

FIG. 3. Seedlings of Sudan grass at the ages of 4, 7, 11, 14, 17, and 21 days respectively. The smallest was excavated on May 26 and the largest on July 12.

had a temperature of 149°F. and the temperature at a depth of 4 inches was 105°F., although it rapidly decreased with depth to 78° at 1 foot. There was no available water in the upper 4 inches of soil, which contained the bulk of the absorbing system. Humidity was only 17 per cent. Although the leaves rolled partly during the hottest part of the day, they recovered at night and growth proceeded steadily.

GROWTH DURING TILLERING

The plants were again examined 4 days later, on June 12. Although the surface soil was quite dry (Table 1) the deeper soil was moist. Atmospheric conditions for growth were favorable and development was rapid. The plants averaged 12 inches in height and had produced three tillers, the oldest about 5 inches tall. The parent plant had 7 leaves and the spread of tops was 11 inches. The leaf area was 14 sq. in. and the dry weight 0.44 gram. The primary root had grown but little, but the secondary root system had made a rapid development. In fact, it exceeded the primary root in depth (Fig. 3F). It consisted of 3 main roots, 22.5, 16, and 11.5 inches in length respectively, and a very young one only 1.5 inches long. The older roots had numerous branches of the first order which spread horizontally. Their absorbing surface exceeded by far that of the primary root system. A rain of 0.72 inch fell on June 12, and replenished the soil moisture (Table 1).

After another 5-day period (June 17), the plants averaged 15 inches high. They had three well developed tillers with an average height of 7 inches. The

TABLE 1. Water content of soil in the N plot in per cent in excess of hygroscopic coefficient to a depth of four feet, and total rainfall between periods of sampling.

Date	0 to 4 Inches	4 to 12 Inches	1 to 2 Feet	2 to 3 Feet	3 to 4 Feet	Inches rainfall
May..24	9.2	11.7	11.9	14.7	15.9	0.00
29	7.8	11.5	12.2	....	....	0.18
June.. 3	5.1	8.4	9.4	....	....	0.00
8	—1.5	6.7	8.7	....	....	0.00
13	10.5	6.1	8.4	14.2	14.7	0.72
19	—3.7	—0.5	5.7	13.3	....	0.00
24	—5.3	—1.9	4.9	11.6	14.2	0.07
29	—6.1	—1.6	0.9	11.8	14.6	0.00
July.. 5	—3.4	—0.7	1.5	13.0	13.7	1.74
7	13.4	0.4	1.0	8.1	12.2	0.66
12	9.5	—0.1	1.2	5.5	9.9	0.55
17	12.9	5.7	0.6	4.4	9.1	1.83
18	14.0	10.9	0.7	4.3	9.2	1.29
22	13.9	7.6	1.2	4.3	8.4	0.44
27	9.8	6.3	0.6	3.8	8.2	0.87
Aug... 1	4.2	2.4	—0.3	3.6	8.2	0.00
7	—1.3	—0.9	—1.0	2.5	7.9	0.03
12	—2.1	—1.5	—1.4	2.3	7.4	0.55
Hygro. Coeff...	10.6	11.1	11.3	8.7	8.6	Total 8.93

primary root had penetrated to a depth of 27 inches. The secondary root system consisted of 9 roots; the longest was 2.5 feet. Most of the secondary roots ran out obliquely at an angle of about 45° to a depth of almost a foot, and then turned somewhat vertically downward. The older secondary roots were densely covered with branches, especially the first foot near the surface of the soil. The lateral spread of the root system averaged 14 inches (Fig. 4A).

When the plants were 30 days old, on June 21, the shoots had nine leaves each and were 2 feet high. The tops had a spread of 21 inches (Fig. 4B). The leaf area was 52 sq. in. and the dry weight of tops averaged 1.59 grams. The primary root had made little growth in the rapidly drying soil (Table 1) but the secondary root system grew very rapidly. It consisted of 13 main roots, the longest slightly exceeding 3 feet. Some of the roots ran rather horizontally outward, others obliqued downward, all into territory unoccupied by the primary root. All of the secondary roots were profusely branched with laterals averaging about an inch in length. The total spread of the root system was 20 inches.

Maturing and Mature Plants

Further measurements were made 11 days later (July 2), but the roots were not excavated. This had been a period of severe drought. The plants had reached a height of 46 inches and had a dozen widely spreading leaves. The panicles were beginning to appear; no new tillers had been formed. The leaf area had increased from 52 to 104 sq. in., and the dry weight from 1.59 to 5.5 grams. The dry weight of the roots obtained from plants grown in the phytometers averaged 2.0 grams.

The development of both tops and roots was again studied 15 days later, on July 17, when the plants were nearly fully grown. Notwithstanding heavy rains, totaling nearly 3 inches since the last examination, the rapid growth had nearly depleted the soil moisture, especially in the second foot of soil, and considerably reduced that of the third foot. The basal leaves had dried and only 7 green upper leaves remained. The total area of the green leaves was approximately 200 sq. in., and the dry weight of the top had increased to 11.4 grams. The parent plant had 2 very small branches and 5 tillers. Three of the tillers were dead. Only one of the tillers and the main stem bore panicles. That of the parent plant was 10 inches long and 7 inches wide; the grain was in the "milk" stage of development (Fig. 5).

The primary root had penetrated to a depth of 4.25 feet and was well supplied with laterals. The secondary root system consisted of 26 main roots. Six had reached a depth of about 5.5 feet; 10 were 3 to 4 feet long; but the remainder were all still in the surface foot (Fig. 6). All except the younger ones were profusely branched throughout to within 6 inches of their tips. The

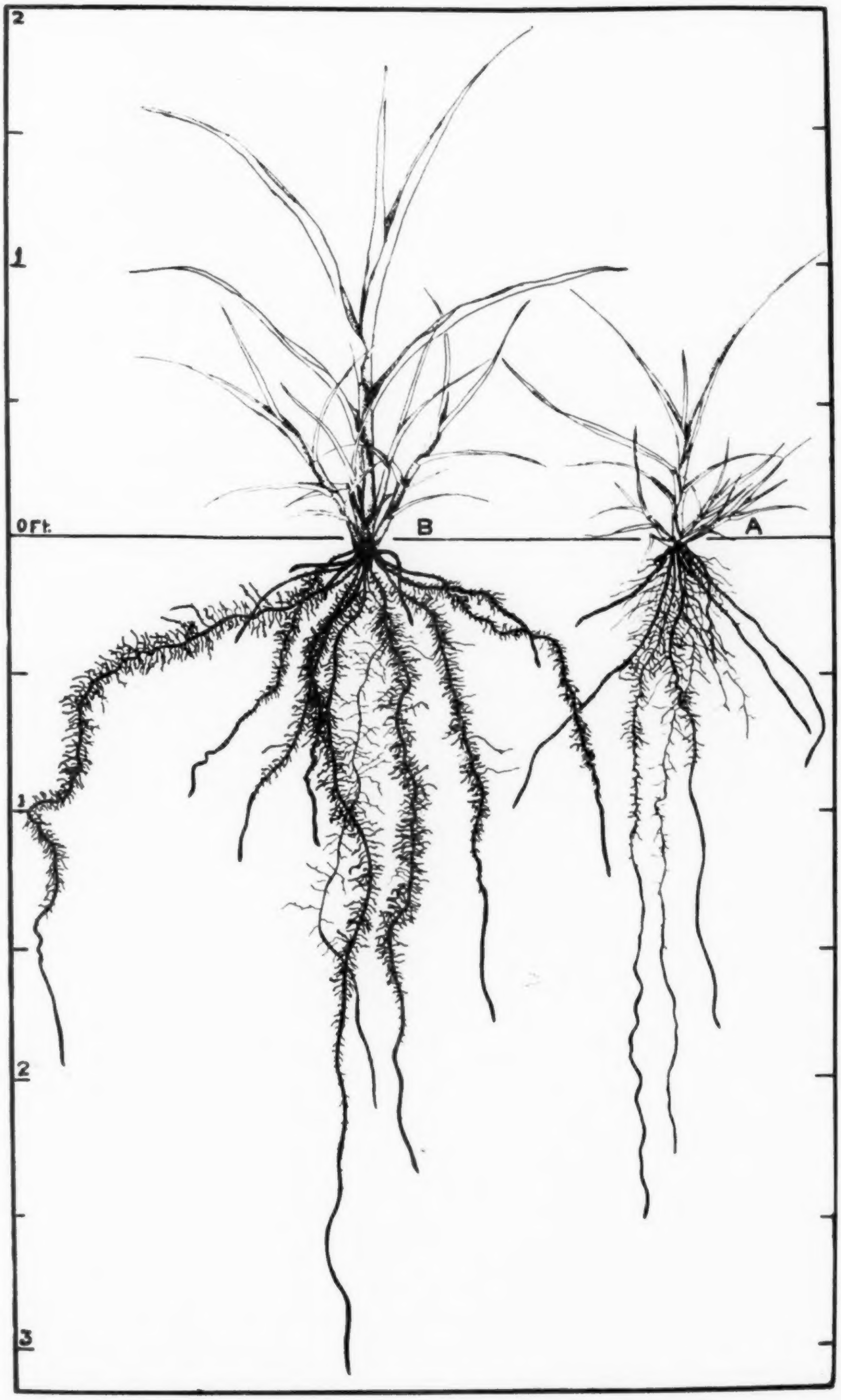

FIG. 4. Development of Sudan grass on June 17 and 21, 26 and 30 days after planting.

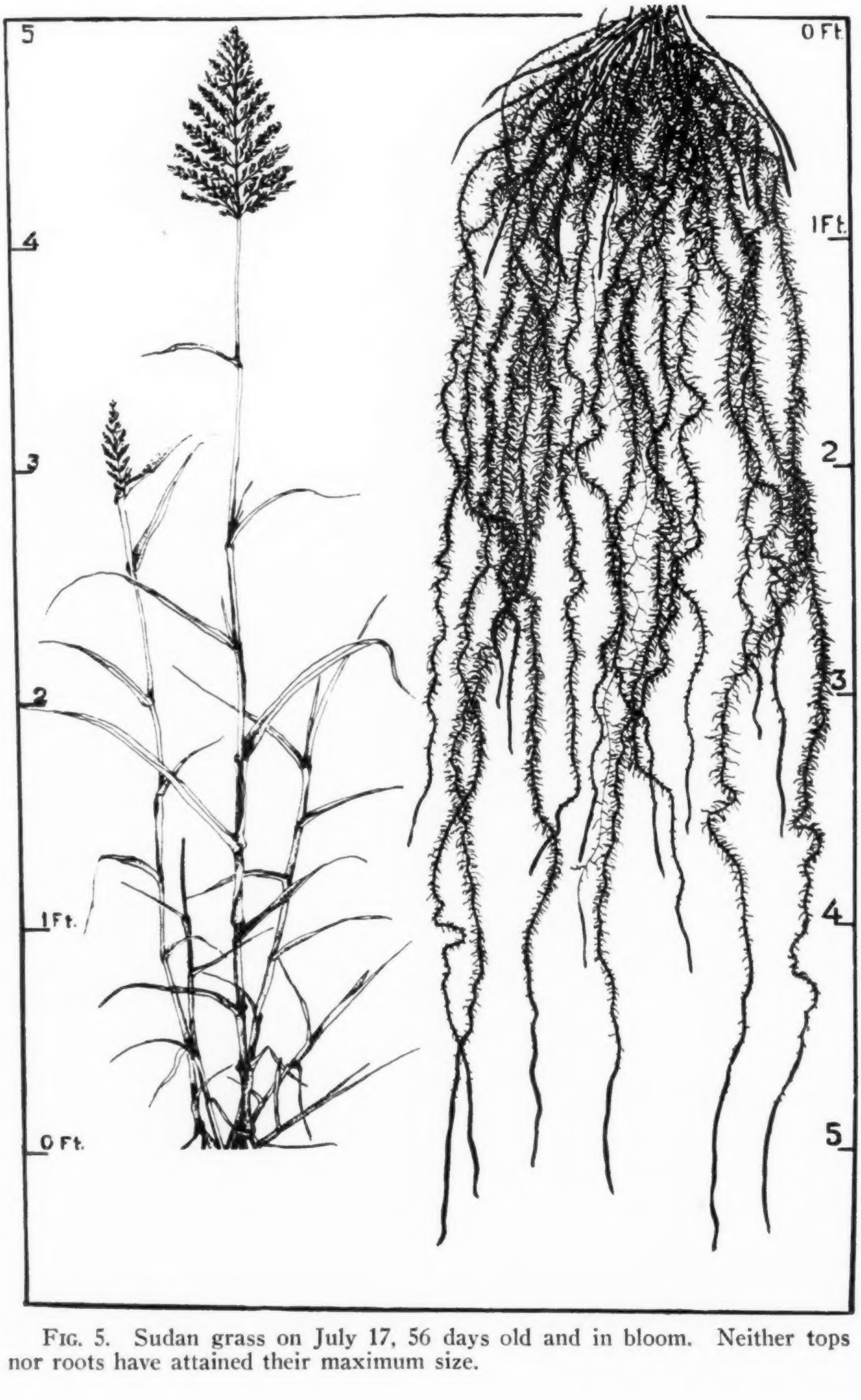

FIG. 5. Sudan grass on July 17, 56 days old and in bloom. Neither tops nor roots have attained their maximum size.

secondary roots at first generally extended obliquely and then turned downward. The whole root system occupied a cylinder of soil 23 inches in diameter and 5.5 feet deep.

The plants were 72 days old on August 2, 17 days after the last examination. Water for growth was exhausted in the second foot, there was only 2 to 4 per cent available in the surface foot, and supplies in the deeper soils had been greatly reduced (Table 1). The shoot had only 6 green leaves although the height was 7 feet. Many of the lower leaves were dry and yellow. The area of the living leaves had scarcely increased. It was 207 sq. in. Only two tillers remained alive, of which one bore a small panicle. The panicle of the parent plant was 12 inches long and 8.7 inches wide. The grain was in the "dough" stage.

FIG. 6. Methods used in excavating roots in the field, although only 56 days old, the Sudan grass had reached a maximum depth of 5.5 feet.

A final study of both tops and roots was made after another 15-day interval, on August 17. The plants were now 87 days old, the seed was ripe, and the crop mature. This development had been hastened by drought. The shoots attained an average height of 7.5 feet. The air dry weight of the grain produced by the parent plant averaged 6 grams. The primary root had penetrated no deeper (4.25 feet) than at the previous excavation 30 days earlier. The secondary root systems consisted of 28 mains roots and their branches. Most of the roots penetrated to about the 4-foot level, but the longest ones to 6.8 feet. The mature root system occupied a volume of soil 2 feet wide and 6.8 feet deep.

Discussion

Sudan grass, introduced into the United States in 1909, has become the most important annual grass for hay. Although it can not be used as a full season pasture grass, since it can not be sown until late in spring and is killed by the first frost, still it is becoming an increasingly important crop for summer pasturage. The stems are coarse but the abundant leaves are rather soft.

Sudan grass is well adapted to drought. When rains came, the seeds germinated promptly and a main root penetrated downward at an average rate of 0.75 inch per day during the first 20 days. At the end of this time the first roots of a very elaborate secondary root system had exceeded the primary root in length. During this period of seedling development, the shoot also made a rapid growth, but it was always exceeded in length by the root system. The general diameter of the root system was blocked out after the first month of growth, and its further development consisted in elongating, branching, and the addition of new roots.

During the second 20-day period root penetration increased to an average of 1 inch per day and new roots were added rapidly. Only at the end of this time, and after tillering had practically ceased, did the length of tops equal the depth of the roots. During the third stage of development, root penetration continued at the rate of 0.8 inch per day, over a period of 47 days. Because of rapid elongation of the shoot and the production of panicles, height of tops exceeded depth of roots throughout this period.

At any time during its growth, this grass can go into a period of semidormancy during extreme drought and revive upon the advent of rains. This probably accounts for the finding of Shevelev (1927) in Russia who states that "during the first month its root system develops faintly." Thus the plant is adapted to drought, first by its rapid germination when water in the surface soil is available, by the rapid development of an excellent absorbing system of great depth and intricate branching which exceeds in extent for a long time that of the tops, and finally by its ability to become dormant and recover after excessive drought.

A mature plant occupied a cylinder of soil 2 feet in diameter and over 6.5 feet deep. There was a single primary root which penetrated to a depth of 4.25 feet, but the secondary root system had 28 main roots. The height of the plant at maturity was about 7 feet. The entire development had been made in slightly less than 3 months.

Because of drought, the increase in area of green leaves was far less than that of the total leaf area. This was due to the dying of the lower leaves as new ones were produced above. Hence, the increase in dry weight of tops occurred at a greater rate than did the area for photosynthesis. Leaf areas during a period of nineteen days during tillering were increased 640 per cent, and dry weight 1155 per cent. Similarly, during the following 32 days the leaf area increased 100 per cent and dry weight of tops 155 per cent (Fig. 7).

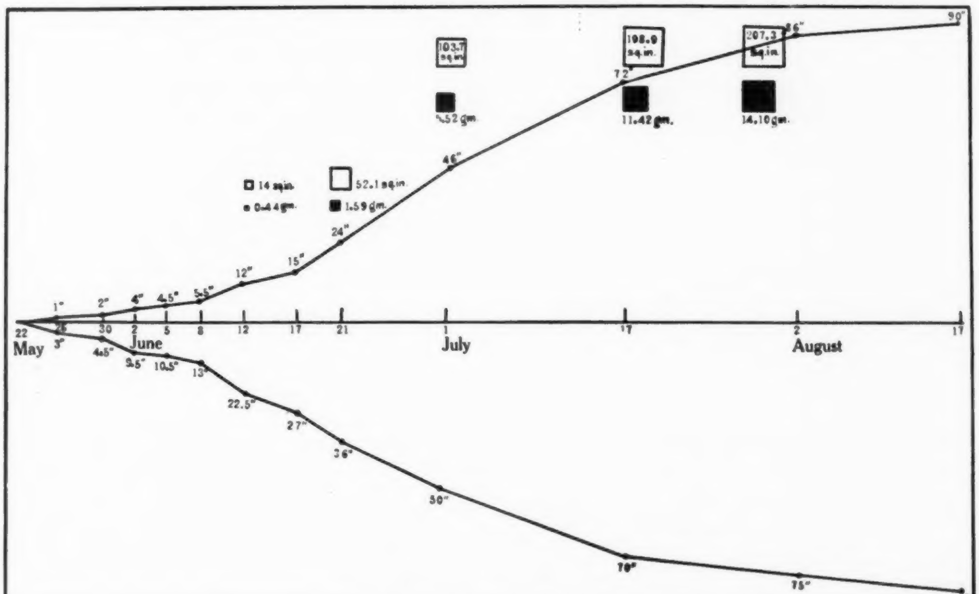

FIG. 7. Relative rate of growth of tops and roots of Sudan grass.

Sudan grass is a heavy consumer of soil moisture. This is due both to its rapid development and to the extensive leaf area resulting from abundant tillering. In addition to using almost 9 inches of rainfall, the crop reduced the original soil moisture practically to the non-available point. Had there been more water available in the upper layers of soil, younger roots could have extended to the deeper layers. These would have more completely exhausted the water in the deeper soil. It seems probable that in addition to the large quantities of water, the crop also made excessive demands on the soil nutrients and thus modified the normal relations of many physical and chemical processes. These reactions deserve special study and until they are understood the use of Sudan grass in crop rotations, especially in dry lands, should be made with caution.

COMPETITION UNDER DIFFERENT RATES OF PLANTING

The seeds germinated promptly and uniformly in all of the plots under the several thicknesses of planting. Conditions for growth were very favorable. Comparisons of the relative development of the plants under each of the several degrees of competition were made at five different intervals. Various measurements of the environmental factors were also made and certain physiological responses determined between these intervals.

Measurements of height indicated that competition had begun by June 9, 18 days after planting, but even on June 12 close observation in the field was necessary to reveal differences in the development of plants.

First Examination

The plants were first measured on June 12, with the results recorded in Table 2.

TABLE 2. Development of plants under the several degrees of competition on June 12.

Criteria	3N	2N	N	½N	¼N
Average height, cm.	25.1	27.3	31.8	32.1	32.7
Average diameter, stem, mm.	3.5	4.7	5.3	5.8	5.9
Average number living tillers	2.0	2.2	2.8	3.0	3.3
Average number leaves	5.9	6.2	7.1	7.3	7.5
Average length of fifth leaf, cm.	20.2	21.1	18.8	18.1	18.2
Average width leaves, mm.	8.9	10.9	10.5	12.3	12.2
Average area, green leaves, sq. in.	5.3	5.5	14.0	19.0	19.3
Average area of stem, sq. in.	1.6	1.8	2.5	3.4	3.6
Average dry weight, grams	0.23	0.33	0.44	0.63	0.68

The data in Table 2 are from 50 representative plants of average size from each thickness of planting. They show a consistent increase in height and diameter of stems from the thickest to the thinnest planting. The average number of tillers increased from 2 to 3.3, and in accord with this there was a small but consistent increase in the average number of leaves. While there were only slight differences in the length of the leaves, which were more attenuated in the thicker plantings, they increased in diameter from the thickest to the thinnest planting, from about 9 to over 12 mm. Marked differences were found in the average leaf area. Plants in the N field had nearly three times more photosynthetic area than those in the 3N, and the increase from the N to the ¼N was 38 per cent. Smaller but somewhat similar differences occurred in area of the stems. Total dry weight of tops from the thickest to the thinnest planting increased threefold.

A rain on June 12 replenished the water content of the dry surface soil (Table 1). Clear weather prevailed. The mean day temperature varied between 82° and 93°F., and the plants grew rapidly. Before the end of the 9-day period, however, all of the available water had been absorbed from the surface foot and the plants were getting their moisture from the subsoil.

SECOND EXAMINATION

A detailed view of the grass under normal rate of seeding, on June 21, together with one of the small phytometers temporarily elevated before a background, is shown in Figure 8. The plants of the phytometer were in every way comparable to those in the surrounding field. At this time 50 plants were again selected from each plot for measuring. Representative plants, approximately conforming to the average measurements, are shown in Figure 9.

The sequence as regards height and diameter of stems was as before, the plants having approximately doubled in height. All had increased in number of tillers, ranging from 20 per cent in the 3N planting to 145 in the ¼N. The number of leaves increased as before with thinness of stand but, so severe was the competition, the thinner plantings now also had the longest leaves. The width of the leaves was about 15 and 23 mm. in the thickest and thinnest plantings respectively. The photosynthetic area was in the same general sequence as before, that in the 3N plot having increased slightly less than 5 times, and that in the ¼N somewhat more than 5 times. It was 24 and 110 sq. in. respectively. The percentage gains in dry weight were 208, 260, 261, 257, and 390 respectively. The weight of the N plants averaged 1.59 grams.

The weather from June 21 to July 1, when measurements were again made, was very dry until a rain of 1.7 inches fell during the last two days of June. The average day temperatures varied between 85° and 95°F., max-

FIG. 8. Detailed view of plot with normal rate of planting and an insert phytometer, on June 21.

imum temperatures often exceeding 100°F. The average day humidity varied between 35 and 45 per cent. Available water content in the N plot was almost exhausted to a depth of 2 feet, but the deeper soil remained moist.

Comparison of Aerial Environmental Factors

The plants were now about two feet tall and each plot presented a different group of environmental factors. Comparative measurements of light intensity, humidity, evaporation, and transpiration were made in each thickness of planting.

Measurements of light intensities were made near noon on a clear day, June 28, at a height of 6 inches above the soil surface. Clements' photometers were employed and the results were expressed in percentages of full light at meridian. The averages of six readings in each plot from 3N to ¼N respectively, were 23, 27, 44, 47, and 60 per cent.

Humidity 4 inches above the soil surface was measured about noon on a cloudless day, July 3. Cog psychrometers were employed and five separate determinations in each plot averaged. The plants in the N plot were nearly 4 feet tall. The air was most humid in the thickest planting (60 per cent), and the humidity decreased to 54, 50, 48, and 46 per cent, in order in the thinner plantings.

Evaporation was determined by placing Livingston's standardized spherical porous cup atmometers 3 inches above the surface of the soil. Each was provided with a non-absorbing device; the period for evaporation extending from June 27 to July 5. The corrected average daily loss in the 3N plot was 18.6 cc.; it increased to 20.1 cc. in the 2N, and to 24.8 cc. in the N. In the thinner plantings losses of 28.9 cc. and 31.3 cc. were obtained.

Fig. 9. Representative plants showing relative development of Sudan grass on June 21; 3N (left) to ¼N (right).

RESULTS FROM PHYTOMETERS

Water loss from phytometers in the 2N, N, and ½N plots was determined during a dry, hot, rainless period, June 24 to 26. Each phytometer had an area of soil surface of 54 square inches. The phytometers were removed from the field, and the containers freed from any adhering soil. They were then weighed and returned to their respective positions in the field, being entirely surrounded by plants of the same thickness of planting. Since the root systems were confined to a somewhat smaller volume of soil, especially as regards depth, than were those in the field, an equal amount of water had been added to each phytometer to compensate. In every case the plants in the phytometers were similar to those in the surrounding field. The phytometers were again weighed at the end of the experiment. The experiment was repeated with a similar set of phytometers on June 28 to 30. In both cases dry weight of tops and roots and volume of roots were determined. The results are given in Table 3.

TABLE 3. Rate of water loss from insert phytometers from June 24 to 26, and from June 28 to 30, and the relative development of tops and roots.

	June 24 to 26 (54 hrs.)			June 28 to 30 (51 hrs.)		
	2N	N	½N	2N	N	½N
Number plants per phytometer	8	4	2	8	4	2
Total water loss, gm.	936	1250	1148	973	1123	1004
Water loss per plant, 24 hrs., gm.	52	139	255	51	118	211
Average dry weight tops, gm.	1.35	2.73	5.14	2.19	4.05	7.67
Average dry weight roots, gm.	0.98	1.90	3.22	1.04	2.07	3.35
Average vol. roots, cc.	9.7	16.7	33.0	9.3	19.5	35.0

Water loss included both transpiration and surface evaporation. Evaporation from the dry soil surface was very little under the cover afforded by the crop. The daily water loss per plant in the two experiments was fairly uniform in the 2N plot. Cloudy weather on June 29, reduced the loss in the N and ½N plantings 15 and 17 per cent respectively. Average water losses per plant from the 2N plantings were 60 per cent less than from the N. The ½N, however, lost 81 per cent more than those of N rate of planting.

The effects of the increasingly severe competition are reflected not only in the dry weight of tops but also in root development. Average weights of tops were in the ratio of 1:1.9:3.6, and the roots 1:2.0:3.2. The volume of roots of plants from the N plots was about twice that of the 2N but only about one-half as great as the ½N.

COMPARISON OF WATER CONTENT

Water content in excess of the hygroscopic coefficient was determined in several plots on June 24 (Table 4).

TABLE 4. Water content in per cent in excess of the hygroscopic coefficient in the several plots on June 24.

Plot	0 to 4 in.	4 to 12 in.	1 to 2 ft.	2 to 3 ft.	3 to 4 ft.
3N	—5.7	—4.4	—1.3	10.7	15.6
2N	—5.6	—2.8	0.6	10.7	14.4
N	—5.3	—1.9	4.9	11.6	14.2
½N	—2.7	1.2	5.8	12.8	15.6
¼N	—2.0	4.2	9.2	15.3	15.9
Hygro. coeff.	10.6	11.1	11.3	8.7	8.6

Examination of Table 4 shows that water in the shallow soil was reduced by absorption and surface evaporation below the hygroscopic coefficient, but to a smaller degree in the progressively thinner plantings. A similar sequence prevailed in the 4 to 12-inch layer of soil except that here water was available in the ½N and ¼N plots. More available water occurred progressively in the thinner plantings in both the second and third foot. This was the greatest depth of root penetration at this time.

GROWTH OF WEEDS

The severity of competition for the factors in soil and air were not only shown in the development of the Sudan grass but also in the development of weeds. These were naturally most troublesome in the thinner plantings where they were continuously removed; very few developed in the 3N or 2N plots. On June 5, when the Sudan grass was well established, 30 sunflower seeds were planted in each plot, the seeds being spaced widely. Germination was prompt and growth at first was vigorous, but there was no time during the summer when the grass was overtopped by the sunflowers even in the thinnest planting. On July 7, when the sunflowers were 32 days old, their height was determined. It averaged, from the 3N to ¼N plot, 15, 16, 21, 24, and 27 inches respectively. The taller plants also had the thicker stems and the larger leaf surface, defoliation of the lower leaves having occurred in the thicker grass.

THIRD EXAMINATION

Further measurements of the development of Sudan grass were made on July 1. Panicles had begun to appear in the thicker plantings, and especially in the 3N where drought was most severe. Because of the large size, only twenty-five plants were selected from each density of planting for detailed study (Table 5).

The data in Table 5 show that the plants in the thickest plot were shortest and those in the thinnest plot tallest. This was also the sequence at the last examination on June 21. The percentage increase in height, since the last measurements, was 71, 77, 94, 98, and 109 in the 3N to ¼N plots respectively.

TABLE 5. Development of plants under the several degrees of competition on July 1.

Criteria	3N	2N	N	½N	¼N
Average height, cm.	88.2	104.0	115.2	122.0	130.0
Average diameter stem, mm.	5.9	6.8	7.6	8.4	10.8
Average number living tillers	3.1	3.4	4.1	6.4	10.2
Average number leaves	11.4	12.0	12.3	12.8	13.0
Average length of third youngest leaf, cm.	43.5	48.5	51.3	54.2	58.0
Average width leaves, mm.	17.4	20.5	24.2	27.6	32.8
Average area green leaves, sq. in.	40.7	46.1	103.7	270.0	405.0
Average area stem, sq. in.	11.2	12.0	12.8	36.9	96.8
Average dry weight, gm.	2.07	3.28	5.52	11.5	19.47

The stem diameter also increased in the same sequence from 5.9 mm. in the 3N plots to 10.8 in the ¼N. There were more than three times as many tillers per plant in the ¼N plot as in the 3N. Leaves in the thinnest plantings were 25 per cent longer and 47 per cent wider than in the thickest. A very great difference occurred in photosynthetic area; the average for the thickest plantings was only 40.7 sq. in. while that of the thinnest was 405. The percentage increase in the several plots since the second measurement was 70, 67, 99, 323, and 268 respectively. The increase from 3N to ¼N in stem area was almost ninefold, and that of dry weight about 10 times.

The period of July 1 to 17 was marked by more moderate temperatures (average day 83° to 90°F.) and higher average day humidities (40 to 65 per cent). Except very early in this period, water was available at all depths as a result of well distributed rains. It was least plentiful at depths of 2 and 3 feet where maximum absorption occurred (Table 1).

COMPARISON OF WATER CONTENT

The grass in all of the plots was growing rapidly and environmental differences in the several plots were becoming more pronounced. Water content in each of the plots was determined on July 7 (Table 6).

TABLE 6. Water content in per cent in excess of the hygroscopic coefficient in the several plots on July 7.

Plot	0 to 4 in.	4 to 12 in.	1 to 2 ft.	2 to 3 ft.	3 to 4 ft.
3N	10.9	—3.1	—2.8	4.4	12.6
2N	13.1	—1.1	0.1	7.1	12.4
N	13.4	0.4	1.0	8.1	12.2
½N	15.0	1.6	4.7	9.3	15.5
¼N	19.1	3.2	8.7	10.0	15.4

Only enough rain had fallen between June 24 and July 7 to moisten the surface 4 inches of soil. The water content at 4 to 12 inches depth had gradually decreased (cf. Tables 4 and 6). Absorption at deeper levels was taking place vigorously; the water content had fallen in the third foot in all

the plots—in the ¼N from 15.3 to 10 per cent and in the 3N from 10.7 to 4.4 per cent. In the fourth foot, considerable reduction of moisture had also occurred but to a smaller degree than in the third foot. At both of these levels the soil was driest in the 3N plot and progressively more moist to the ¼N plot where the highest water content occurred.

Comparative Root Development

A study of root development was made on July 11 and 12 in the 3N, 2N, N, and ½N plots by means of the trench method (Table 7). The locations of the trenches in the several plots are shown in Figure 1.

Table 7. Root development of Sudan grass under different degrees of competition on July 12.

Plot	Depth, inches	Total spread of roots, inches	Number roots, secondary root system	Working level
3N	66	9	16	Root tips mostly at 2-foot level; many at 4-foot level; a few at 5 feet.
2N	66	14	18	do
N	68	23	27	Root tips D. distributed from first to sixth foot, most abundant at 4-foot level.
½N	70	28	38	Similar to N.

The data in Table 7 show that the roots in the thinner plantings were better developed than those in the thicker ones. Root penetration, spread of roots, and number of roots of the secondary root system were all least in the thickest planting. They gradually increased with thinner plantings, reaching a maximum in the ½N plot. Thus competition underground was least in the thinnest stand and severest in the thickest one.

Several roots of average length and diameter were selected from the 3N, N, and ¼N plots for anatomical study. The object was to determine the effect of competition upon size and structure of the individual root. The roots were all taken in the third foot of soil, on July 11 and 12. They were cut into sections convenient for killing and fixing in chromoacetic acid solution. After embedding in paraffin, cross sections 12 microns thick were cut and stained in safranin and counterstained with fast green. The averages of a large number of measurements are given in Table 8, and representative root sections in Figure 10.

Even causal examination of Figure 10 shows the profound effect of competition upon root structure. Roots from the 3N plot had the smallest total diameter and the smallest diameter of both cortex and stele. Those from the N plot were largest. With a decrease in the density of planting, the ratio of

TABLE 8. Diameter and area of cortex and stele of roots of Sudan grass.

Criteria	3N	N	¼N
Diameter of root, microns	844	1242	1772
Width of one side of cortex, microns	190	290	426
Diameter of stele, microns	464	662	920
Cross-sectional area of root, sq. mm.	0.550	1.211	2.465
Area of cortex, sq. mm.	0.390	0.867	1.801
Area of stele, sq. mm.	0.160	0.344	0.664
Ratio of area of stele to area of cortex	1:2.4	1:2.5	1:2.7

the area of stele to the area of cortex gradually increased. Stated conversely, the area of the cortex was smaller in proportion to the area of the stele as the density of planting increased. This reduction in the size of both cortex and stele resulted from reduction in the size of the individual cells, rather than from a decrease in their number.

COMPARISON OF STRUCTURE OF LEAVES

Representative leaf materials were collected in the 3N, N, and ¼N plots on July 17, when the plants were nearly fully grown. The leaves were taken from the parent plant (not the tillers) at a height of 18 inches from the soil

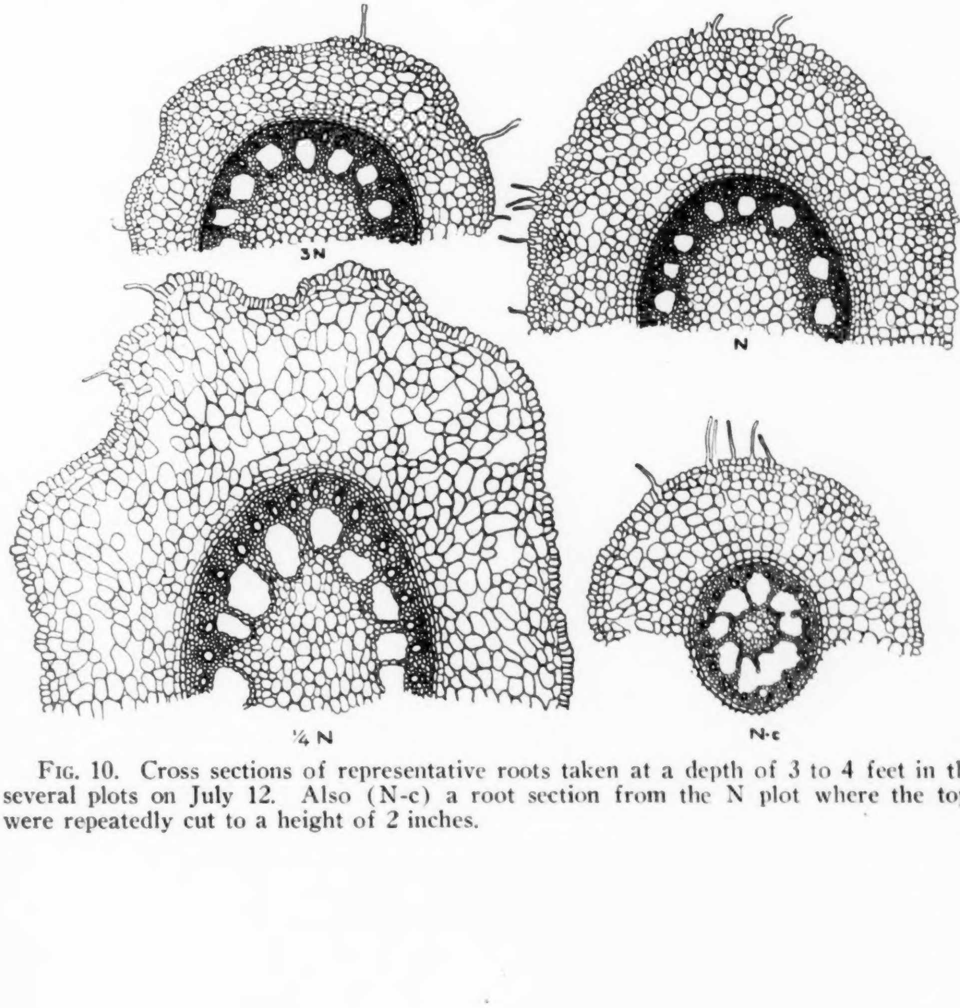

FIG. 10. Cross sections of representative roots taken at a depth of 3 to 4 feet in the several plots on July 12. Also (N-c) a root section from the N plot where the tops were repeatedly cut to a height of 2 inches.

surface. These leaves had received the full impact of the factors of competition for a considerable period of time. Sections 5 mm. square were cut from the blade of the leaf 20 cm. from the ligule and half way between the midrib and the outer edge. They were treated as were the root materials, the cross sections being 10 microns thick. After extended measurements the sections in Figure 11 were selected as representative.

The leaves from the 3N plot were only 103 microns in thickness, those from the N 125, and those from the ¼N 143. The bundles were both larger and farther apart in the thinner plantings, the average distance being 35, 42, and 51 microns respectively. In general, the effects of competition as exhibited by leaf structure in smaller size, closeness of veining, and small compacted cells were those of drought.

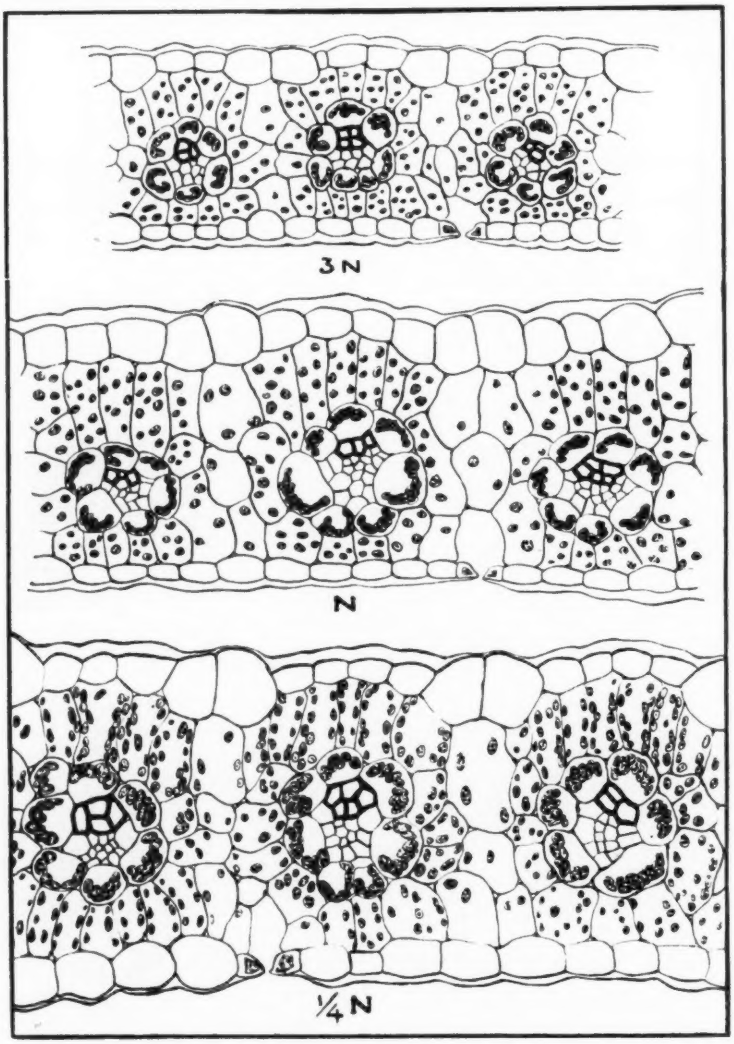

FIG. 11. Representative cross sections of leaves of Sudan grass from the several plots on July 17.

RESULTS FROM PHYTOMETERS

Water loss, from the large phytometers, was determined for a third time on July 15 to 21. Each had a depth of 2.5 feet and an area of soil surface of 76 sq. in. The plants in the large phytometers were about 6 feet tall and had a total photosynthetic area of approximately 200 sq. in. (Fig. 2). The weather was mostly sunny with moderate temperatures but the water losses were relatively high.

TABLE 9. Rate of water loss from phytometers from July 15 to 21, and relative development of tops and roots.

Criteria	2N	N	½N
Number of plants per phytometer	22	9	5
Total water loss, grams	11,560	9,002	8,430
Water loss per plant, 24 hrs., grams	87.6	166.7	281.0
Average dry weight tops, grams	8.0	12.0	38.3
Average dry weight roots, grams	5.3	7.5	18.2
Average vol. roots, cc	22.8	35.0	100.2

Table 9 shows that for a given soil area the total water loss in the 2N plot was greatest and that in the ½N was least. This resulted from the greater number of plants per unit area in the 2N planting. The amount of water lost per plant was greatest in the ½N plot where the plants were fewest but largest. The loss per plant in the 2N plot was 48 per cent less than from the N, but the plants in the ½N plot lost 68 per cent more. The increase of dry weight of tops from 8 to 12 and then to 38 gm. was marked, but scarcely more so than the dry weight and volume of the roots under the different densities of planting. The ratios of dry weight of roots to tops in the 2N, N, and ½N plants were 1 to 1.5; 1 to 1.6; and 1 to 2.1 respectively. Thus the roots had suffered a relatively smaller decrease than the tops, a fact that may be attributed to the greater development of roots in the thicker plantings as a result of the drier soil.

FOURTH EXAMINATION

The development of Sudan grass in the several plots was again determined on July 17, after a period of 17 days (Fig. 12). The panicles had developed rapidly beginning July 1 and were mostly unfolded after 7 to 10 days. Their development was most rapid in the 3N plot but decreased regularly with wider spacing, being longest delayed in the ¼N plot.

The plants of the thickest plantings were smallest in every way; there was a progressive increase in all measurements of size and weight with decreased thickness of stand, the ¼N plantings showing the greatest development. The average area of green leaves, for example, increased from the 3N to the ¼N planting in the ratio of 1:1.7:4.1:7.9:13.3. This dwarfing of stature is at-

FIG. 12. Representative plants showing development of Sudan grass in the 3N (left), 2N, N, ½N, and ¼N (right) plots on July 17.

tributed directly to the decrease in light and water, and probably in part to nutrients.

During the next interval, July 17 to August 2, average day temperatures were about 85°F. The average day humidity was 58 to 72 per cent. Two heavy showers maintained a supply of water in the surface foot of soil, but the deeper soils were gradually being depleted of their moisture except the fourth foot (Table 1).

COMPARISON OF AERIAL ENVIRONMENTAL FACTORS

At this time the plants in the N plots were about 6 feet tall. Comparative measurements of light intensity, humidity, and evaporation were made in each thickness of planting.

The average of six readings of light intensity taken at a height of 6 inches above the soil, in the 3N to ¼N plots respectively, were 11, 13, 25, 27, and 32 per cent. The light intensities at this time were only about half as great as those from similar readings taken 23 days earlier when they were, in the above sequence, 23, 27, 44, 47, and 60 per cent.

Humidities on July 19, 4 inches above the soil surface were 77, 74, 69, 69, and 66 per cent in the 3N to ¼N plot respectively.

RELATIVE GROWTH OF SUNFLOWERS

A second measurement of the development of the sunflowers was made on July 28, 3 weeks after the first. All of the plants in the 3N plots had succumbed (Fig. 13).

The increasingly greater development of all parts of the plants with an increase in water and light, as the Sudan grass became thinner, shows clearly the harmful effects of competition upon the individual. The height increased gradually with reduced competition from 41 to 64 inches, the diameter of stem from 6 to 25 mm., the number of green leaves from 7 to 24, and the total leaf area from 2.42 to 112.08 sq. dm. respectively.

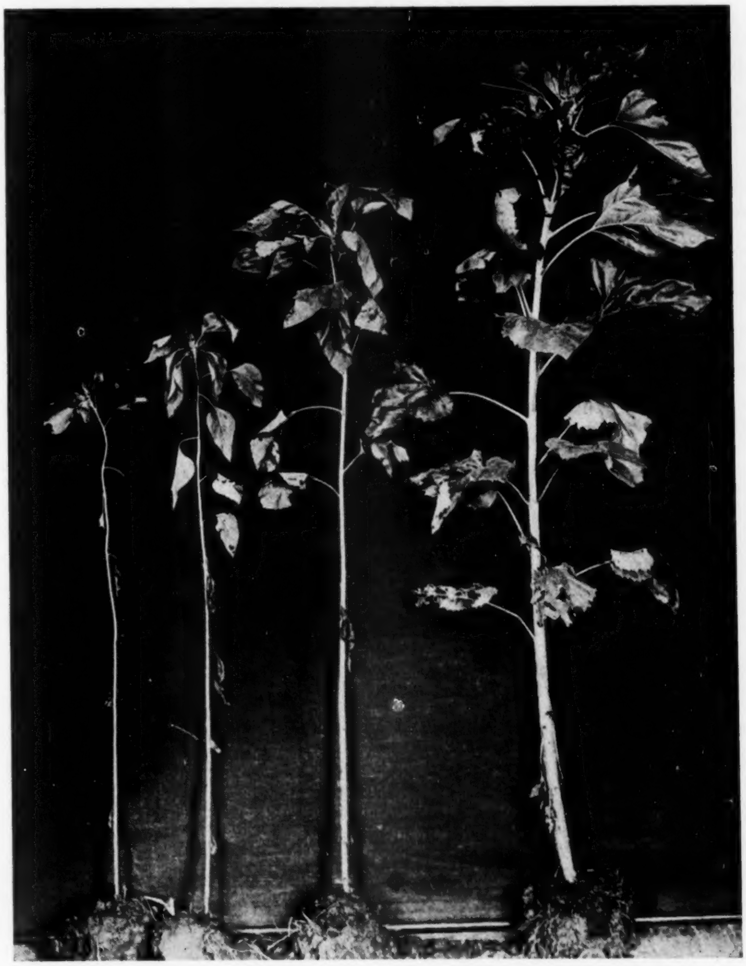

FIG. 13. Sunflowers of average size from the 2N (left), N, ½N, and ¼N (right) plots, respectively. The largest is 64 inches high.

The dense shade was unfavorable to chlorophyll development and the sunflowers in the thicker plantings were yellowish green in color. This was probably aggravated by a shortage of nitrogen (cf. Clements, Weaver, and Hanson, 1929). In the 2N plots all but the top leaves were dead. A determination of the starch content of the leaves was made at the end of a clear day. The leaves from the several plots were all selected at the same height—that of the living leaves of the sunflowers in the 2N plot. Sach's iodine test revealed the fact that the plants in the 2N plots were making very little starch, but the amount rapidly increased with the more favorable conditions in the thinner plantings. From the standpoint of weed control, the competitive effects of the Sudan grass are clearly beneficial.

Osmotic Pressure

A sufficient quantity of leaves of Sudan grass for triplicate determinations of the osmotic pressure of the sap was collected at 4 o'clock on the afternoon of July 27. Only leaves of parent plants at a height of 3.5 feet from the ground were selected in each of the several plots. They were frozen for 24 hours in an ice-salt mixture after which the sap was expressed under pressure of 10,000 pounds by means of a Carver press. Freezing-point determinations were then made and the results were expressed in atmospheres by referring to the Gortner and Harris, (1914) table of osmotic pressures. The osmotic pressures increased with decreased thickness of planting as follows: 10.6, 11.9, 12.8, 13.0 to 14.2 atmospheres respectively. Since water was plentiful, at least in the surface foot and in the deep soil (Table 1), the response of the plants as recorded in differences in osmotic pressure seemed to be correlated with differences in the light intensities and consequently the ability to manufacture sugars. Similar determinations in the N plot when the plants were but 18 days old gave an osmotic pressure of 17.1 A., but this was at a time when water content in the surface soil was low, temperature extremely high, and the air very dry.

Fifth Examination

When the grain was beginning to ripen on August 2, 16 days after the last examination, plants were again selected and the usual measurements obtained. At this time the crop was 72 days old (Table 10).

Because of the production of panicles, all of the plants had gained somewhat in height. The increases in the several plots from 3N to ¼N were 10, 11, 18, 21, and 17 per cent respectively. The 3N and 2N showed decreases of 7 and 14 per cent in their area of green leaves, but the N, ½N, and ¼N plots had made gains of 4, 14, and 9.3 per cent during the 16 days. Gains in dry weight occurred in all of the plots. They were, in sequence, from the 3N to ¼N, 15, 17, 24, 63, and 43 per cent.

TABLE 10. Development of plants under the several degrees of competition on August 2.

Criteria	3N	2N	N	½N	¼N
Average height, cm.	187.0	199.2	215.0	230.0	240.0
Average diameter stem, mm.	3.7	4.6	5.7	6.7	9.0
Average number living tillers	0.5	1.2	2.3	5.3	8.0
Average number living leaves	4.0	4.9	5.5	6.0	6.0
Average length of third youngest leaf, cm.	45.5	49.7	56.0	56.4	59.4
Average width leaves, mm.	21.5	23.9	25.9	31.0	38.0
Average area green leaves, sq. in.	44.3	72.9	207.3	428.1	692.3
Average area stem, sq. in.	21.3	24.3	40.1	99.0	250.0
Average dry weight, grams	8.39	9.84	14.10	53.00	109.99

From this time until harvest, on August 17, somewhat lower temperatures prevailed. A rain of 0.55 inch on August 8 was again followed by dry weather. The dry air caused high transpiration losses and the demands of the crop for water exceeded the supply, except in the deeper soil (Table 1).

Comparative Root Development

The final study of root growth was made on August 17 and 18 when the plants were harvested. Depths of penetration in the 3N, 2N, N, and ½N plots were 74, 78, 82, and 90 inches and the total spread of roots 9.6, 16, 24, and 32 inches. Thus the root system had been dwarfed somewhat in proportion to the tops. Marked differences were also found in the number of roots of the secondary root system. They were as follows: 17, 19, 28, and 44. In the thickest planting, many of the secondary roots ended in the second foot of soil. But with decreased competition and increased available water a larger number of the roots extended deeper.

Mature Plants

The crop matured rapidly during the second week in August. Even the plants in the ¼N plots were drying, and those in the thickest plantings were very dry.

Production of Branches and Panicles

Previous to harvesting the crop, on Aug. 17, the degree of branching of the parent plants above ground was ascertained in the several plots. The average number of branches increased with wider spacing of the plants as follows: 0.2, 1.2, 1.6, 2.8, and 3.2.

The number of panicles per plant varied greatly in the several plots. In the 3N and 2N plots competition was so severe that the parent plants alone produced seed. In the N plots an average of 2 panicles was produced, 4 in the ½N, and 8 in the ¼N.

Fifty panicles were selected from parent plants in each plot and the average length and width ascertained as well as the dry weight of the grain (Fig. 14 and Table 11).

TABLE 11. Development of the panicles of Sudan grass from the several plots on August 18.

Criteria	3N	2N	N	½N	¼N
Length of panicle, cm.	25.3	28.2	30.2	33.7	37.5
Width of panicle, cm.	14.9	22.5	25.9	28.1	31.5
Air dry weight of grain, gm.	3.62	4.07	6.15	9.55	13.87

Table 11 reveals a direct decrease in the length and width of the panicle with an increased rate of planting. The decrease in dry weight of grain, however, was even more pronounced than that of the panicle. While the panicles decreased 33 per cent in length and 52 per cent in width from the ¼N to 3N, the decrease in yield of grain per panicle was 73 per cent.

YIELDS

In harvesting the crop, it was cut at a height of 2 inches above the surface of the soil. To avoid border effects, only 200 square feet from the middle of each plot was used (Hulbert, Mitchels, and Burkart, 1931). The few weeds that persisted were excluded. After drying for a single day in the field, and before shattering of the seed occurred, the plants were removed to the laboratories where they were thoroughly air dried and then weighed. The yield was greatest (18,786 gm.) from the N plot and least (13,582 gm.) from the ¼N. The next lowest yield (16,530 gm.) occurred in the ½N plot. Thus decreasing the number of plants by ½ reduced the yield only 12 per cent, while a decrease in seeding to ¼ reduced it by 27 per cent. Conversely, doubling the rate of sowing decreased the yield (2N, 18,548 gm.) only 1.0

FIG. 14. Representative panicles from the 3N (left), 2N, N, ½N, and ¼N (right) plots. The largest is about 15 inches long.

per cent, and tripling the amount of seed reduced it (3N, 17,606 gm.) 6 per cent.

The yields per acre were, in order of increasing thickness of planting, 3.25, 3.96, 4.50, 4.44, and 4.22 tons respectively.

DISCUSSION

Clements, Weaver, and Hanson (1929) state that "two plants do not compete as long as the water content and nutrients, the heat and light are in excess of the needs of both. The moment, however, that the roots of one enter the area from which the other draws its water supply, or the foliage of one begins to overshade the leaves of the other, the reaction of the former modifies unfavorably the factors controlling the latter, and competition is at once initiated." The intensity of competition is directly correlated with the degree of development of the different organs of the plants—stems, leaves, and roots. The same investigators state that "the outcome as indicated by the number, size, and form of the plants concerned is a good measure of the intensity of competition." Also that the "effect of competition finds expression in the functions, structure, or form of the individual or of the community."

The degree of competition for water, light, and probably for nutrients as well was clearly illustrated by the results obtained from Sudan grass grown under the five different rates of planting. The first panel in Figure 15 shows the relative heights of the plants in the several plots at various stages of development. Differences in height were not marked, except the 3N planting, until July 1, at the time of stem elongation when competition for light was severe. The more crowded the plants the less able were they to secure sufficient materials to develop as greatly in height as plants in the less crowded, adjoining plot. Thus throughout their growth and at maturity the height increased with thinness of stand.

Competition was not alone for light but especially for water. Available water was always least in amount in the 3N plot and greatest in the ¼N. Thus there existed a direct correlation between the height of shoot and water content. This is explained by the findings of Weaver and Clements (1929), "when the soil is very dry, root development is greatly retarded or even ceases, and the above ground parts are consequently dwarfed."

During the first 5 weeks of growth the reduction of roots in the thicker plantings was nearly in proportion to that of tops. But later the roots showed a greater development than the tops in response to the drying soil and great need for increasing supplies of water.

The diameters of the stems increased regularly with thinness of planting. The maximum, attained on July 1, was 5.9 mm. in the 3N plot and 10.8 in

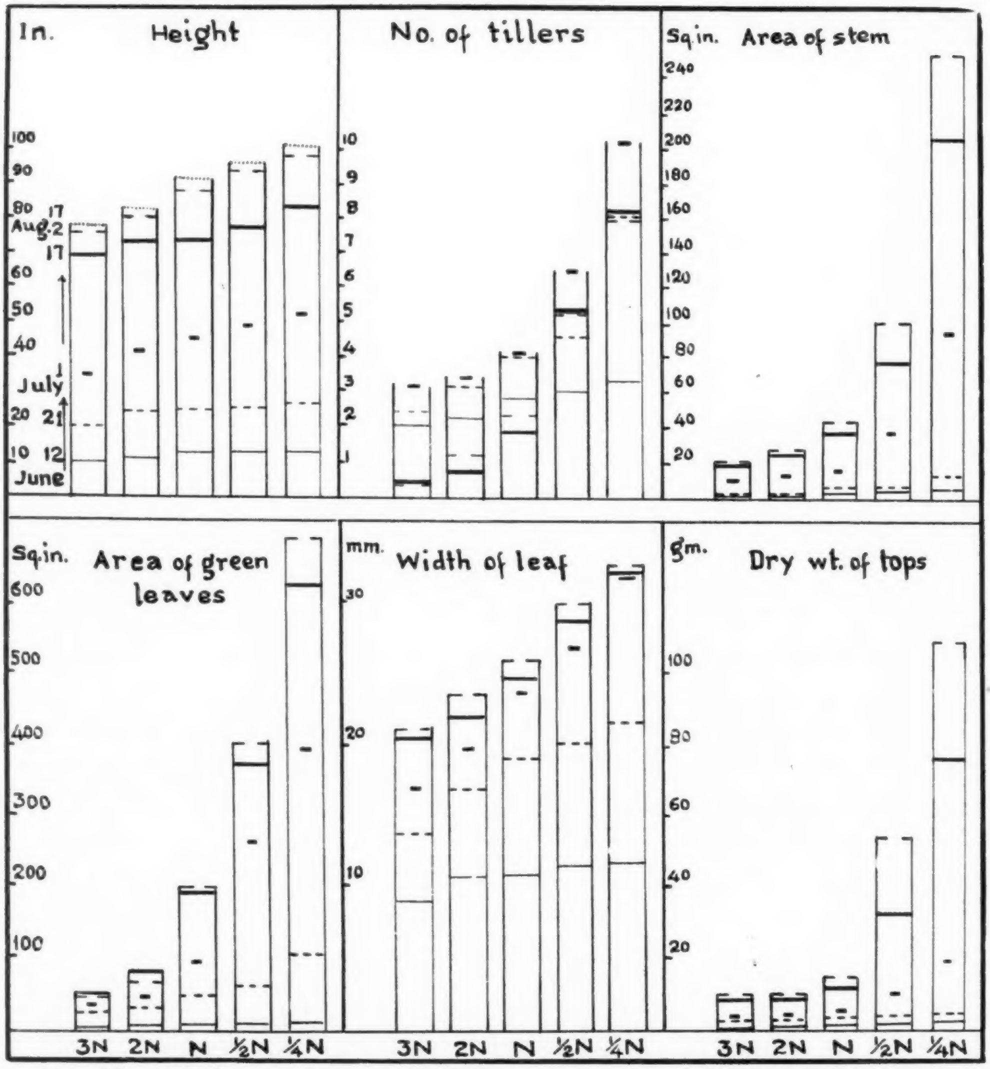

FIG. 15. Relative development of Sudan grass under the different thicknesses of planting.

the ¼N. From thence to maturity, with the drying of the bases and maturing of the plants, there was a steady decrease.

The number of tillers produced from the several plots increased with thinness of planting. The maximum number of living tillers occurred when the plants were 40 days old on July 1. In the sequence of thinness of planting, they were 3, 3, 4, 6, and 10 respectively. The number of living tillers decreased from this time until harvest. This was due to dryness of the soil and partly to insufficient light reaching these new shoots, especially in the thicker plantings.

The differences in the area of the stems from the several plots were far more pronounced than the differences in height. There was a direct correla-

tion between area of stem and density of planting. The increase in the area of stems from 3N to ¼N at maturity was more than twelvefold.

The length of the leaves was greatest in the thinnest planting and the width of the leaves also increased with fewer plants per unit area. Likewise the relative area of green leaves and dry weight of tops from the several plots showed the same trend of behavior. The total leaf area per square meter (10.7 sq. ft.) of soil on June 12 was greatest in the 3N (13.5 sq. ft.) and diminished somewhat regularly to 2.5 sq. ft. in the ¼N. The decrease amounted to 81 per cent.

By June 21, the leaf area in the 3N plot had increased over 4 times, but that in the ¼N nearly 6 times. Assuming that no plants had died by July 1, the leaf area per square meter of the 3N plot was slightly less than doubled (104 sq. ft.) while that in the ¼N had increased almost 4 times (47.7 sq. ft.). The thinnest planting thus had nearly 45 per cent as great a leaf area as the thickest, although it had only 5.2 per cent as many plants. With the great increase of tillers in the thinner planting and their death in the thicker ones, it seems certain that the final leaf area in the ¼N greatly exceeded that of the 3N. Conditions in the other plantings were intermediate.

The average green leaf area per plant was determined for each plot by adding the areas obtained at each of the five examinations and dividing by 5. From these data and the average dry weight per plant on August 2, the dry weight in grams produced per square inch of green leaf area was determined. This was, from the 3N to ¼N plantings, 0.26, 0.20, 0.12, 0.22, and 0.29 gram respectively.

Thus it appears that the well lighted and well watered plants in the ¼N plots were most efficient, and that there was a marked decrease with thickness of planting until the N plot was reached. With a reduction of the green leaf area in the thicker plantings, due to the death of the leaves to near the top of the stems, the efficiency of the remaining younger and better lighted leaves increased. This viewpoint is supported by a study of relative production of dry matter in relation to green leaf area at the time of each of the five examinations. Except during the extreme drought of June, the same sequence was determined in every case.

The water loss, in grams per square inch of green leaf area per day, was greater in the ½N and less in the 2N than in the normal planting during the seedling stage (June 21). The values were 1.8, 3.1, and 3.7 from thicker to thinner plantings. But during the stage of elongation (July 1) the losses were 1.0, 1.1, and 0.8. At maturity, when the plant had received the full impact of drought, losses were greatest in the thickest or most xeric plot and least in the thinnest or most mesic one. The losses were 1.0, 0.8, and 0.7 gram, respectively. This is in accord with the theory of xerophytism as proposed by Maximov (1931).

Results of anatomical study of leaf sections from 3N, N, and ¼N plots reveal the fact that the leaves were thinnest in 3N, and thickest in ¼N. These findings are supported by Weaver and Clements (1929) who state that "the thin leaves present an increased surface in proportion to tissue involved, for the reception of diffuse light." The much smaller area of green leaves and the smaller dry weight of the individual plants in the 3N plot than in the thinner planting were due to a combination of low light intensity and reduced water supply. Brenchley (1919) states that "the decrease in light caused by overcrowding is a most potent factor in competition even when an abundance of food supply and water is presented to each individual plant." This is in accord with the results of Clements, Weaver, and Hanson (1929) that "with light intensity reduced five times, the leaf area was decreased a third, and the dry weight three times in *Helianthus* and *Triticum*." They state further that "the amount of photosynthate for the 'thins' was 50 per cent larger than for the 'thicks,' the sequence being in agreement with that of density and light values."

Considering the greatest yield, which occurred in the N plot, as 100 per cent, it was reduced 6 per cent by tripling the rate of planting but 27 per cent by decreasing the rate to one-fourth. Thus it appears that under excessive competition more forage was produced than where the plants were too widely spaced. Stated in terms of factors of water and light, it seems clear that the thickest plantings utilized all that were available while in the thinnest plantings, even after maximum tillering, both water and light were often in excess of the demands. They were less so in the ½N where the yield was reduced only 12 per cent; yields in the 2N were reduced only 1 per cent. Thus as stated by Brenchley (1919) "it is generally recognized that up to a certain point, it is profitable to give growing crops plenty of room, but beyond this limit the total yield is apt to fall off."

Had yield of grain been used as the criterion the percentages would probably have been different, but the same general principles would have held. Kiesselbach and Anderson (1925) found that during a period of three years, when Sudan grass was seeded at 10, 20, 40, and 80 pounds per acre at Lincoln, Nebraska, the weight of 100 stalks averaged 1.46, 1.14, 0.94, and 0.72 pounds, respectively. The relative diameters of the stems at the base were, in the same sequence, 0.17, 0.16, 0.14, and 0.11 inch. Chemical analysis showed that the grass did not differ materially in composition even though the coarseness of the forage was decidedly reduced by closer spacing. The yields they obtained from upland soil near Lincoln were very similar to those in this experiment. They varied somewhat with the stage of cutting, from 3.26 tons per acre when cut as the first heads were appearing to 5.04 tons when mature.

Each thickness of planting presented a different set of environmental factors. In the thicker plantings, the surface of the soil was fully covered with

leaves and the loss of water through surface evaporation was low. The relative humidity was fairly high due to the fact that the moisture laden air surrounding the plants was not so rapidly changed by wind movement as was that in the thinner plantings. This environment tended to reduce transpiration. But the large number of plants per unit area of soil (324 per square meter in the 3N as against 17 in the ¼N plot) far more than overshadowed these conditions and resulted in total water losses increasing directly in proportion to thickness of sowing. Phytometers were very useful in measuring these losses directly and quantitatively.

EFFECTS OF CUTTING ON SUDAN GRASS

Sudan grass is frequently used in temporary pastures since it grows well during midsummer when bluegrass and certain other pasture grasses do not thrive. In these experiments one strip 15 feet wide and another 20 feet wide extended at right angles across all of the major plots with different thickness of planting. Plants in the narrower strip were cut at a height of 2 inches and those in the wider one at 6 inches height at six different times throughout the summer (Fig. 1). The purpose was to simulate grazing and thus study the behavior and yields of the plants cut 2 and 6 inches high. While all the plots were cut on the same days, the intervals between cuttings were determined by the growth of the plants. In order to avoid the so called "border effects" (Arny and Hayes, 1918; Kiesselbach, 1919), the yields from only the central 100 square feet of each plot were determined, although the whole plot was cut uniformly and the forage removed. After clipping the entire plot at the proper height, by means of a grass shears, the yields from this central portion were carefully gathered, air dried, and weighed. The last cutting was made on August 18, at the time when the larger, unclipped plots were also harvested. This permitted of a comparison between the sums of the partial yields from each clipped plot with the total yield from the plots where the plants grew undisturbed.

FIRST CUTTING

The first cutting was made on June 22 when the plants in the N plot were 24 inches tall. At this time only, the higher cutting was made at the 9-inch level. Weeds were suppressed in the thicker plantings by the competition of the Sudan grass. Among the more widely spaced plants, they were regularly removed by pulling. Hence, no weeds were included in the harvest (Table 12).

Even casual examination of Table 12 reveals the fact that the yield steadily decreased with thinness of planting. In plots clipped high, the extremes were 299 and 73 grams; in those clipped closely 773 and 233 grams.

TABLE 12. Successive yields from 100 square feet in the several plots cut 6 and 2 inches high respectively; total yields from unclipped plots; and decrease in total forage production resulting from clipping.

Date of clipping	3N		2N		N		½N		¼N	
	6-in.	2-in.	6-in.	2-in.	6-in.	2-in.	6-in.	2-in.	6-in.	2-in.
	gm.	gm.	gm.	gm.	gm.	gm.	gm.	gm.	gm.	gm.
June 22	299	647	276	773	215	641	142	379	73	233
29	557	306	776	464	759	372	729	313	501	269
July 8	472	642	459	758	504	622	541	478	465	438
20	928	410	904	428	903	513	872	430	861	415
Aug. 1	848	370	848	382	850	499	825	416	795	412
12	181	102	205	209	293	276	275	264	250	202
18	2046	0[1]	2137	0	2368	0	2161	0	1525	0
Total forage produced, gm.	5331	2477	5605	3014	5892	2923	5545	2280	4470	1969
Forage, unclipped plots	8803		9274		9393		8265		6791	
Per cent decrease from clipping	39	72	40	68	37	69	33	72	34	71

[1] On August 18, plants in all plots were cut at a height of 2 inches. Those in the closely cut plots had died.

RESULTS FROM PHYTOMETERS

The effects of cutting on water loss and root development in relation to tops were determined by the use of insert phytometers between June 24 and 26. These had been installed, each with 4 plants, at the time of planting in the N plots to be cut 2 inches high and 6 inches high as well as in the unclipped N plots. The total water losses from the plants and 54 square inches of soil surface under the several conditions, respectively, were 482, 995, and 1250 grams. The average dry weight of tops and roots were, in the same order, 0.39 and 0.48 gm.; 1.58 and 0.92 gm.; and 2.73 and 1.9 gm. This was 5 days after the first cutting. These data show that root growth was progressively less with more severe cutting. Moreover, in the closely cut plot, root weight exceeded the weight of the tops. Root volume had been reduced as a result of clipping; the average volumes were 0.48, 0.92, and 1.9 cc. respectively.

SECOND CUTTING

The plants recovered rapidly and made a good growth, especially those clipped high. At the second clipping on June 29, the yields of the taller plants were greatly in excess of those harvested 7 days earlier (Table 12). This was due in part to the closer clipping, which was 6 inches. The greatest yield was no longer from the 3N plot but from the 2N, otherwise the sequence was the same as before. This sequence also held for the closer clippings, the 2N yielding most. In all cases but one, the yields were less than previously, the ¼N alone giving an increased yield.

RESULTS FROM PHYTOMETERS

The effect of clipping on root development was again ascertained from a second lot of phytometers on June 26. These were all from the 2N plots; the plants in two of them had now been clipped twice, 8 and 1 days previously. Dry weight of roots were in the ratio of 100:79:53 as compared to 100:84:61 in the N plots only 4 days earlier (Table 13). Thus one effect of clipping was greatly to retard root growth.

TABLE 13. Relative root development in the several plots as affected by cutting the tops.

Date	Number of cuttings	Plot	DRY WEIGHT		VOLUME	
			gm.	Relative	c.c.	Relative
June 26..........	0	N, uncut	1.9	100	16.7	100
	1	N, 6-in.	1.59	84	13.7	82
	1	N, 2-in.	1.16	61	8.2	49
June 30..........	0	2N, uncut	1.04	100	9.3	100
	2	2N, 6-in.	0.82	79	6.9	74
	2	2N, 2-in.	0.55	53	4.6	49
July 21..........	0	N, uncut	3.23	100	17.0	100
	4	N, 6-in.	2.39	74	13.0	77
	4	N, 2-in.	0.68	21	6.0	35
July 21..........	0	½N, uncut	4.55	100	26.0	100
	4	½N, 6-in.	3.13	69	20.5	79
	4	½N, 2-in.	0.94	21	6.5	25

THIRD CUTTING

A third cutting was made on July 8. Although a heavy rain had fallen on June 29 and 30 yet it only temporarily replenished the water in the surface soil. Drought prevailed at least in the thicker planting (Table 6). This undoubtedly reduced the yields.

The highest yield of the 6-inch cutting, 541 grams, was in the ½N plot, and the lowest, 459 grams, in the 2N. There was no regularity of sequence. The highest yield of the 2-inch cuttings was, as before, in the 2N plot. The 3N yielded less, and there was a constant decrease to the thinnest planting. The closely cut plots yielded more than the 6-inch cuttings in all of the thicker plantings, but in the ½N and ¼N they yielded less (Table 12).

COMPARATIVE ROOT DEVELOPMENT

The relative root development under the several conditions in the normal plots was determined by direct excavation on July 11 and 12. The depth of penetration in the unclipped plots, those clipped high, and those clipped closely was 68, 58, and 51 inches respectively; the lateral spread was 23, 20, and 20 inches. The number of main roots of the secondary root system de-

creased from 27 to 16 and then to 14. The root tips of the unclipped plants were found distributed more or less uniformly to a depth of nearly 6 feet; on plants clipped high they did not extend much beyond 4 feet; and in the closely clipped group they were largely in the second and third foot. Roots of the closely clipped plants showed a weakened condition and deterioration throughout (Fig. 10 N-c). The average diameter of the roots of the uncut N-plants was 1.24 mm., that of the plants cut closely was 0.78 mm., which was only 63 per cent as great. The average diameter of the stele was 0.662 mm., and 0.320 mm. in the two lots of roots respectively.

Relative Water Content of the Soil

Water content of the soil in all of the plots of the N planting was determined on July 18 (Table 14).

TABLE 14. Water content in per cent in excess of the hygroscopic coefficient at various times in the N plots.

Date	Plot	0 to 4 in.	4 to 12 in.	1 to 2 ft.	2 to 3 ft.	3 to 4 ft.
July 18	Unclipped	14.0	10.9	0.7	4.3	9.2
	Clipped at 6 inches	15.3	13.4	0.7	9.2	11.4
	Clipped at 2 inches	16.6	15.0	1.3	10.0	12.4
July 27	Unclipped	9.8	6.3	0.6	3.8	8.2
	Clipped at 6 inches	7.2	8.9	1.3	6.2	10.6
	Clipped at 2 inches	6.1	10.3	4.0	8.7	11.7
Aug. 7	Unclipped	—1.3	—0.9	—1.0	2.5	7.9
	Clipped at 6 inches	—1.8	0.3	0.7	5.8	10.2
	Clipped at 2 inches	—3.0	1.7	2.5	8.7	12.0

Table 14 shows that there was more water available in the clipped plots than in the unclipped ones. Moreover, water content was higher in the plots where clipping was close and the transpiring surface most reduced.

A rain of 1.2 inches fell on July 7-8 and another of 1.7 inches on July 12. Following these rains water was available at all depths in the N planting, although before the second rain none was available in the surface 4-12 inches of soil (Table 1).

Fourth Cutting

A fourth cutting was made on July 20, after a period of 12 days. Of the plots cut 6 inches high, the 3N gave the highest yield (928 gm.). Yields decreased in the sequence of thinner plantings, the ¼N yielding 861 gm. Among the closely cut plants the N yielded highest, 513 gm., the dry weights decreasing regularly both towards the thinnest and towards the thickest plantings (Table 12).

RESULTS FROM PHYTOMETERS

Immediately following the fourth clipping, on July 21, studies were made on the average dry weight and volume of roots in the three subplots of the N planting. The roots were obtained from large phytometers each of which presented a soil surface of 76 square inches and contained 4 plants. The dry weights, from uncut to closely cut plants, were 3.23, 2.39, and 0.68 grams respectively, and the ratio 100:74:21. Thus the clipped plants had fallen far behind their rate of development under the same conditions after the first clipping when the ratio was 100:84:61 (Table 13). The ratio of the volume of the roots had changed from 100:82:49, on June 26, to 100:77:35, somewhat over three weeks later.

The retarded development of the root systems under the clipping treatment was further shown by roots obtained from similar phytometers from the ½N plots. These data, which are very similar to the preceding, are shown in Table 13. In every case the more closely clipped tops developed the poorest root systems.

DEGREE OF TILLERING

The effect of clipping on development of tillers was determined. The number of tillers on ten of the largest plants selected from each subplot is shown in Table 15.

TABLE 15. Number of tillers on ten largest plants from each of the several plots on July 26.

Plot	Average	Range	Per cent
3N, uncut	3.0	2 to 4	100
3N, 6-in.	16.2	12 to 21	540
3N, 2-in.	20.6	15 to 30	686
2N, uncut	3.5	3 to 4	100
2N, 6-in.	20.2	13 to 29	634
2N, 2-in.	27.1	20 to 33	774
N, uncut	4.5	4 to 5	100
N, 6-in.	25.9	17 to 33	575
N, 2-in.	33.2	22 to 43	737
½N, uncut	6.5	6 to 8	100
½N, 6-in.	48.1	30 to 62	586
½N, 2-in.	52.0	41 to 76	800
¼N, uncut	12.0	8 to 16	100
¼N, 6-in.	54.3	40 to 83	452
¼N, 2-in.	59.4	86 to 88	494

Data in Table 15 show a stimulating effect of clipping upon the production of tillers. The unclipped plants had fewer tillers than the clipped ones, and those clipped closely more than those clipped high. The data also show clearly that tillering increased directly with increased spacing between plants.

Relative Number and Size of Plants

The relative number and size of living plants were also determined in three selected square meters in each of the closely cut, 3N, N, and ¼N plantings. The number of living plants was 195, 76, and 14 in the above sequence, and the dead ones 21, 14, and 1. In the 3N plots there were no plants with more than 40 tillers; 48 per cent had 20 to 40 such off-shoots, and 52 per cent had less than 20. In the N plot the percentages were in the above sequence 6, 39, and 55 but in the ¼N, 60, 20, and 20. Thus while tillering was high in all of the plots it was greatest in the most open stand.

Similar counts in the subplots of the N planting showed that the number of living plants was about the same (80 per sq. m.) in all. But the number of dead plants increased per unit area with closeness of clipping. The degree of tillering also increased in the same sequence. No plant with more than 20 tillers occurred in the unclipped plots; 38 per cent were found among those clipped 6 inches high, and 44 per cent (some with more than 40 tillers) grew in the closely clipped plots.

Relative Water Content of Soil

Nine days later, July 27, another determination of water content was taken in the normal planting (Table 14). Except for the surface layer, the unclipped plants had more thoroughly exhausted the water supply to a depth of 4 feet. The plants clipped high had reduced the water content to a greater degree than the closely clipped ones. The slightly smaller water supply in the 0 to 4 inch layer in the closely clipped plots was due to greater evaporation from the surface soil.

Rate of evaporation from a free water surface was determined by placing 4 soil cans, 7 cm. in diameter and 4.5 cm. deep, each containing 100 cc. of water on the ground in each plot. The average water loss per day during three clear, calm days (July 27-30) was 10, 23, and 40 cc. in the N plots unclipped, clipped high, and clipped closely, respectively.

Fifth Cutting

A fifth cutting was made on August 1. Under both heights of cuttings the greatest yields were from the N plot. Yields from the several plots cut 6 inches high were remarkably uniform, only that from the ¼N being somewhat low. All showed a lower yield than at the preceding cutting, probably because the plants were greatly weakened. The yields from the close cutting were far from uniform and higher in the thinner than in the thicker plantings, where the plants withstood cutting best (Table 12).

Eleven days later, on August 7, water content was again determined in the N plots (Table 14). From an examination of Table 14 it is apparent that drought prevailed during the period from July 27 to August 7. Prac-

tically all of the water available for growth was exhausted from the first two feet of soil on August 7. Eleven days earlier, 6 to 8 per cent was available to the 4-inch level and 6 to 10 per cent in the remainder of the surface foot. A study of Table 14 shows that considerable absorption occurred in the third foot (except in the closely clipped plot) but very little in the fourth. Except in the portion of the soil most affected by surface evaporation, the water content, as before, increased directly with the degree of clipping of tops.

SIXTH CUTTING

When the sixth cutting was made on August 12, the water content in the N plot had been reduced to the nonavailable point to a depth of 2 feet (Table 1). The third foot was quite dry and the crop was ripening. In all cases the yields were much lower than for the preceding period (Table 12). The highest yields from both cuttings were found again in the N plots. The yield of the 6-inch cutting was higher than that of the 2-inch one except in the 2N plot where it was only slightly less (Table 12). The yields of the 6-inch cuttings, from the thickest to the thinnest plantings, were only 21, 24, 35, 33, and 31 per cent as great as that of August 1, eleven days earlier. The 2-inch cutting, in the same order, yielded 28, 55, 55, 63, and 49 per cent as much respectively, as before. These decreased yields were due to the weakening or death of the plants, conditions favored by the drought.

MATURE CROP

Dry weather continued, water content was further reduced, and the crop ripened somewhat prematurely. The clipped plants suffered severely and made little growth before drying.

EFFECT OF CUTTING ON ROOT DEVELOPMENT

A study of the relative root development in the N plots was made at the time of harvest, August 17 and 18. The root system in the uncut field reached a depth of 82 inches; in the plot clipped at 6 inches height it penetrated to 67 inches, but in the closely clipped one to only 56. Small differences were found in lateral spread; the spread was about 3 inches less in the clipped plots. Differences in the number of secondary roots were marked, decreasing with severity of cutting from 28 to 19 and then to 16. It was also ascertained that the roots of the plants clipped 6 inches high had died back to about the 4-foot level and those closely clipped to about 3 feet. Great differences in diameters of roots were also found (Fig. 10 N-c).

YIELDS

The closely cut plants had died back after the sixth clipping without further growth. The large yields of the plots cut 6 inches high were due to the

last cutting being made at 2 inches height, in order to obtain the total production of forage.

The total yield from the unclipped plots was greatest from the N rate of planting. Considering this as 100 per cent, the other yields were, 2N, 98 per cent; 3N, 93; ½N, 88; and ¼N, 72 per cent.

The total forage produced by the plants cut at 6 inches height was, in order of amounts, N, 2N, ½N, 3N, and ¼N. Comparing the total yields of the 6-inch cuttings with those of the unclipped plots of similar densities the losses from thickest to thinnest plantings were 39, 40, 37, 33, and 34 per cent respectively.

The most forage produced from the 2-inch cuttings was from the 2N plot, with decreasing yields in the following order: N, 3N, ½N, and ¼N. The total decrease in yield was greater from the 2-inch cuttings than from the plants cut at 6 inches height. Compared to the yields from the 3N to ¼N unclipped plots, the decreases were 72, 68, 69, 72, and 71 per cent. Thus while the decrease in total yield averaged about 37 per cent for the plants clipped high, the average where the plants were clipped closely was 70 per cent.

Discussion

A study of the graphs showing the yields produced at each cutting reveals several pertinent facts (Fig. 16). The plants cut at 2-inches height yielded most in the 2N plots during the first three clippings, but in the N ones during the last three. Thus an average increase in yield of 22 per cent was gained by doubling the rate of planting, but after the third clipping there was none. Maximum yields from the plots cut 6 inches high were less consistent, shifting from the 3N through the 2N to the ½N and then back to the 3N. After the third cutting, however, the yields from the several plots were fairly uniform, except the last, the two thinnest plantings consistently yielding somewhat less.

After the plants had once been clipped, the new growth yielded more where they had been clipped high than where they had been clipped closely. An exception occurred in the N and more thickly planted plots at the third cutting, but the causes were not evident. General differences in yields at each cutting varied because of unequal periods for growth between cuttings, environmental conditions, and degree of exhaustion of the plants. The greater yields from the higher cuttings are to be explained upon the basis of the greater photosynthetic area retained after cutting. At the time of the first cutting the shoots were two feet high and the root systems were growing vigorously and probably had little accumulated food. There were 13 main roots, the longest being about 3 feet.

Repeated cutting back of the shoot stimulated tillering. Once formed, the tillers were least injured by successive cuttings and developed bushy

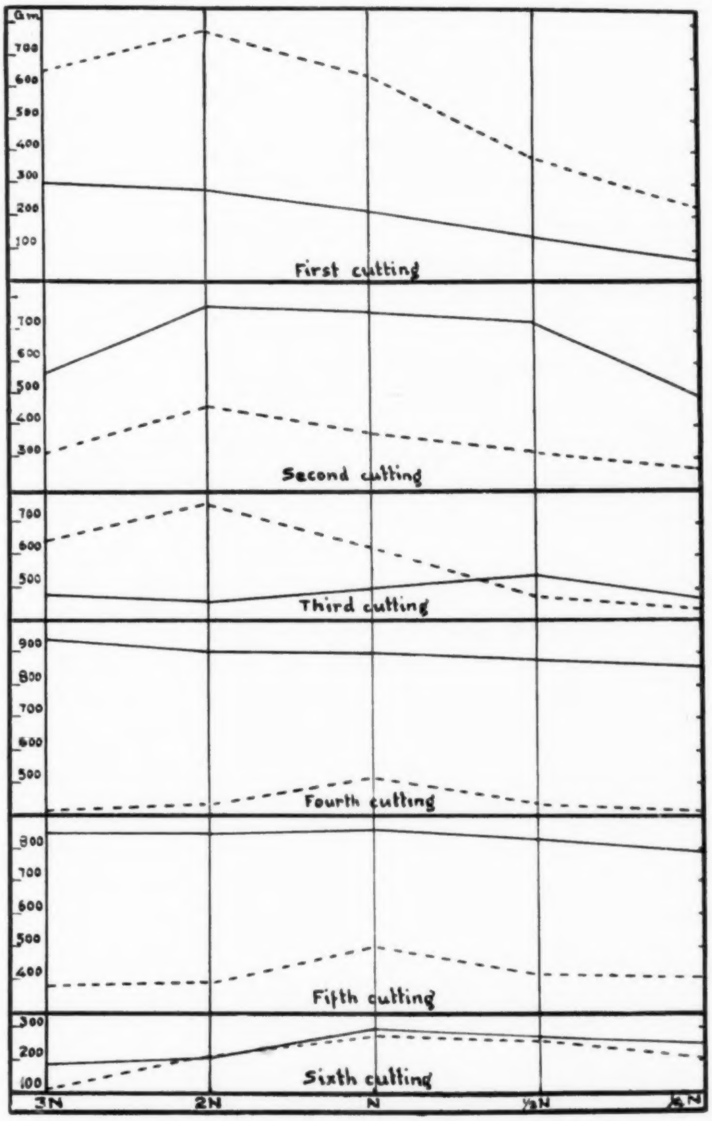

FIG. 16. Yields from 100 square feet of each plot at the several cuttings. Solid lines rèpresent cuttings at 6 inches height, except the first which was 9 inches; broken lines, cuttings at 2 inches height.

plants. After two or three clippings the stem of the mother plant died. After the fourth cutting, tillering was greatest in the closely cut and least in the uncut plots. The greater degree of tillering in the closely clipped plots was due to the development of latent buds at the basal nodes, many of which could not have grown had the supplies of food materials and foods been used in the production of a large parent stem. The repeated clippings also harmed the growing tillers until finally the plants died of starvation and drought. Drying of the surface soil was accentuated by the removal of weeds. But

under normal conditions they would have competed for water and finally overtopped the Sudan grass. Harrison (1931), and Biswell and Weaver (1933) state that the deleterious effect of frequent cutting may, however, be offset partially by cutting the plants at a greater height above the ground.

Sudan grass is a strong competitor of weeds. This is due to its rapid growth and great height. The leaves are quite tolerant of shade, remaining green at the 12-inch level in the 3N plot after rough pigweed, crab grass, and cultivated sunflowers had succumbed. A decided advantage of moderate grazing is that of weed control.

The extent of root development correlated with the extent of tops. The uncut plants increased their dry weight of roots 70 per cent from June 26 to July 21, a period of 26 days. The roots of plants cut 6 inches high four days before June 26, and thrice more before July 21, showed an increase of 50 per cent during this 26-day period. But where the tops were cut 2 inches high at these same periods, the dry weight of the root decreased 41 per cent (Table 13). In the last case, although a few new roots were added in the surface soil, the established roots died back from their tips for a considerable distance in the deeper soil. Sturkie (1930) found that any cutting treatment of *Sorghum halepensis* L. reduces the rootstock development, and the more frequently the cuttings were made the greater was the reduction. This was due to depletion of food reserves in the roots. Aldous (1930) has shown that "cutting frequently or cutting at maturity depletes the reserves in the roots of herbaceous plants."

The effect of clipping of the tops of Sudan grass not only affected the amount of dry weight of the roots, but also the extent of root penetration, size, and number of roots of the secondary root system. This is in accord with the findings of Robertson (1933) who states that removal of tops invariably retarded root penetration and sometimes stopped it completely. Biswell and Weaver (1933) also found that the roots of the clipped grasses yielded only 2.6 to 20.6 per cent as much as unclipped ones. They were also smaller in diameter than were those of the controls. The diameters of the roots of frequently cut *Poa pratensis* L. and *Panicum virgatum* L. were only 76 and 64 per cent respectively as great as those of the controls.

There was but slight difference in the total spread of the roots of the uncut and cut plants. This was due to the fact that when the first cutting was made on June 22, the lateral spread of the roots had already reached a maximum, the general area for root penetration being nearly blocked out (cf. Weaver, 1926). The number of mature roots per plant varied greatly, from 28 in the control to 19 in those clipped high and to only 16 in those clipped closely.

The leaf area of the tops was somewhat in proportion to the available water content of the soil as well as to the available light. Results of repeated

determinations of the water content in the uncut plots showed that where drought was greatest, in the soil layer in which the roots were distributed, the leaf area was least.

The effects of competition were accentuated by the dry summer and the relationships between factors and plant development were probably more marked than they would have been had the season been one of abundant rainfall.

SUMMARY

Sudan grass was grown on level, deep, fertile, sandy loam soil at Lincoln, Nebraska, during the dry, hot summer of 1933. Its life history was determined under the normal rate of planting, the effects of competition under different rates of planting, and the behavior of plants under different heights of cutting.

Planted on May 22 at the rate of 22 pounds per acre, development was so rapid that during the 20 days of the seedling stage the roots grew at an average rate of 0.75 in. per day and the tops developed 7 leaves and reached a height of 13 in. The length of the single primary root (13 in.) was exceeded by the first roots of an elaborate secondary root system, and the general area to be occupied by the roots was blocked out.

During the following 20 days of tillering, the roots grew an inch per day and reached a depth of 4.1 ft. In extent, they still exceeded the tops, which were 3.8 ft. tall and had developed 4 tillers, the first appearing 17 days after planting.

A height of 7.5 ft. and a root depth of 6.8 ft. were attained during the following 47 days of flowering and maturation. Rate of root growth decreased to 0.8 in. per day, the mature root system, consisting of 28 main roots, occupying a volume of soil 2 ft. wide and 6.8 ft. deep. Only one of the 5 tillers bore a panicle; that of the parent stalk was 12 in. long and produced 6 grams of grain.

Increase in dry weight (to 14.1 grams when in flower) always exceeded the increase in area of green leaves (maximum, 207 sq. in.), since, owing to drought, most of the lower leaves died.

This grass is adapted to drought by its prompt germination when water is available, by its rapid root penetration into the deeper soil, and by its ability to become dormant during drought and recover thereafter.

Sudan grass is a heavy consumer of water, due to its rapid development and great leaf area resulting from abundant tillering. Although 9 in. of rain fell during its 87 days of growth, the moist soil at the time of planting had lost practically all of its available water at harvest.

Competition, in plots 25 by 40 feet each, was measured under normal rate of sowing (N), 2N, 3N, ½N, and ¼N rates. Differences in height

were not marked until rapid stem elongation occurred about July 1. The less crowded the plants the more able were they to manufacture materials for growth of stems, hence the plants became increasingly taller from the 3N to the ¼N plots. The same relationships attained, throughout the entire period of development, as regards length, width, and area of leaves, diameter and area of stems, number of tillers, size of panicles, and dry weight of tops, as well as number and depth of roots.

Length of mature leaves varied from 18 in. (3N) to 23.7 in. (¼N), and width of leaves from 22 mm. to 38 mm. The maximum area of green leaves (Aug. 2) was 44.3 sq. in. per plant in the 3N plot and 692.3 sq. in. in the ¼N. The average area of green leaves per square meter, on July 1, was 104 sq. ft. and 47.7 sq. ft. The thinnest planting had nearly 45 per cent as great an area of leaves as the thickest, but only 5.2 per cent as many plants.

Leaves in the thicker plantings were much thinner, the veins were more closely spaced, and the cells much smaller than in the thinner plantings. Osmotic pressure of cell sap of leaves increased progressively from 10.6 A. (3N) to 14.2 A. (¼N).

Diameter of stems ranged from 5.9 mm. (3N) to 10.8 mm. (¼N). The range in average height was from 6.2 feet to 8 ft., but the range in area of stems was far greater, from 21.3 sq. in. in the 3N to 250 sq. in. in the ¼N.

The maximum number of tillers varied from 3 in the 3N to 4 in the N and 10 in the ¼N.

The average length of panicles varied from 25.3 cm. (3N) to 37.5 (¼N); the width from 14.9 to 31.5 cm., and dry weight of grain from 3.6 to 13.9 grams.

The reduction in growth of roots in the thicker plantings was nearly in proportion to the reduction of tops during the first five weeks, but later, as a response to the drying soil, roots showed a greater development than the tops. Depth of penetration ranged from 74 in. (3N) to 90 in. (¼N); spread of roots from 9.6 to 32 in.; and number of main roots from 17 to 44. Roots were of smaller diameter in the thicker plantings, ranging from an average width of 0.884 mm. (3N) to 1.77 mm. (¼N).

Water losses from large, insert phytometers, were greatest both per unit area and per plant with increased thinness of planting. Losses per unit area of green leaves were greatest in the thinner stands during the seedling stage but later they became greater in the thicker plantings.

Repeated determinations of available water content of soil showed uniformly that competition for this factor was most severe in the thickest planting and progressively less so to the thinnest. Water was a chief limiting factor for growth; the degree of plant development was in direct relation to the amount of available water.

Light ranged from 23 to 60 per cent from thickest to thinnest plantings

when the plants were about 46 inches tall, but from 11 to 32 per cent when they had attained full stature. Relative humidity decreased with thinness of planting, evaporation also increased.

The yields of cured hay per acre in the order of thickness of planting were (¼N) 3.25, 3.96, 4.50, 4.44, and 4.22 tons respectively; considering the N yield 100 per cent, they were 72, 88, 100, 99, and 94 per cent.

Plots 20 by 25 feet in each thickness of planting were cut 6 times at a height of 6 inches, and another lot (15 x 25 feet) at 2 inches. Maximum partial yields from plots cut 2 inches high were from the 2N or N plantings; those from the 6-inch cuttings varied widely. After the plants had been clipped once, subsequent yields were greatest from those that had been clipped high.

Repeated cuttings of the tops caused the death of the parent stalk and stimulated tillering, plants cut closely tillering most. Due to its rapid growth and great height, Sudan grass is a strong competitor of weeds, but its repeated cutting favors their development.

Extent of root development correlated with extent of tops. Increase in dry weight of roots was 70, 50, and —41 per cent in the N uncut plants, those cut high, and those cut closely, respectively, during a period of four cuttings.

The uncut plants had 28 main roots; those cut at 6 inches height, 19, and those cut at 2 inches height, 16. The last, which were much smaller in diameter, had died back from the tips. These closely cut plants finally died of starvation and drought. Use of water, especially below 2 ft., was least in the closely clipped plots, and greatest in the unclipped ones.

The total yields decreased as a result of clipping 6 inches high, from 3N to ¼N, 39, 40, 37, 33, and 34 per cent. Decreases where the clipping was at 2 inches height were 72, 68, 69, 72, and 71 per cent.

LITERATURE CITED

Aldous, A. E. 1930. Effect of different clipping treatments on the yield and vigor of prairie grass vegetation. Ecology, **11**: 752-759.

——— **and J. W. Zahnley.** 1931. Tame pastures in Kansas. Kans. Agri. Exp. Sta. Bull. No. 253.

Arny, A. C. and H. K. Hayes. 1918. Experiments in field technic in plot tests. Jour. Agr. Res., **15**: 251-262.

Biswell, H. H. and J. E. Weaver. 1933. Effect of frequent clipping on the development of roots and tops of grasses in prairie sod. Ecology, **14**: 368-390.

Brenchley, W. E. 1919. Some factors in plant competition. The Ann. App. Biol., **6**: 142-170.

Clements, F. E., J. E. Weaver and H. C. Hanson. 1929. Plant competition. Carnegie Inst. Wash. Pub. 398. Pp. 10-11; 288; 312; 318-319.

Gortner, R. A. and J. A Harris. 1914. Notes on the calculation of the osmotic pressure of expressed vegetable saps from the depression of the freezing point, with a table for the values of P for $\Delta = 0.001°$ to $\Delta = 2.999°C$. Amer. Jour. Bot., **1**: 75-79.

Harrison, C. M. 1931. Effect of cutting and fertilizer applications on grass development. Plant Physiology, **6:** 669-684.

Hughes, H. D. and F. S. Wilkins. 1926. Sudan grass. Ia. Agr. Exp. Sta. Bull. 233.

Hulbert, H. W., C. A. Mitchels and F. L. Burkart. 1931. Border effect in variety tests of small grains. Idaho Agr. Exp. Sta. Res. Bull. No. 9.

Kiesselbach, T. A. 1918. Studies concerning the elimination of experimental error in comparative crop tests. Nebr. Agr. Exp. Sta. Bull. No. 13.

1919. Plant competition as a source of errors in crop tests. Jour. Amer. Soc. Agron., **11:** 242-246.

1923. Competition as a source of error in comparative corn yields. Jour. Amer. Soc. Agron., **15:** 199-215.

——— **and A. Anderson.** 1925. Annual forage crops. Nebr. Agr. Exp. Sta. Bull. No. 206.

———**, A. Anderson and W. E. Lyness.** 1928. Tillage practice in relation to corn production. Nebr. Agr. Exp. Sta. Bull. No. 232.

———, et. al. 1933. Standards for the conduct and interpretation of field and lysimeter experiments. Jour. Amer. Soc. Agron., **25:** 803-828.

Maximov, N. A. 1931. The physiological significance of the xeromorphic structure of plants. Jour. Ecology, **19:** 273-282.

Montgomery, E. G. 1910. Oats; variety tests; rate of sowing; cultivation. Nebr. Agr. Exp. Sta. Bull. 113.

1912. Competition in cereals. *Ib.,* 127.

Robertson, J. H. 1933. Effect of frequent clipping on the development of certain grass seedlings. Plant Physiology, **8:** 425-447.

Sturkie, D. G. 1930. The influence of various top-cutting treatments on rootstocks of Johnson grass *(Sorghum halepense).* Jour. Amer. Soc. Agron., **22:** 82-93.

Shevelev, J. N. 1927. The biological particulars of growth of root system Sudan's grass. East-Stepp Provincial Agr. Exp. Sta. U. S. S. R. 34.

Weaver, J. E. 1926. Root development of field crops. McGraw Hill Book Company, Inc., New York. Pp. 253-261.

——— **and F. E. Clements.** 1929. Plant Ecology. McGraw Hill Book Company, Inc., New York. Pp. 222; 262-273; 312-315; 339.

——— **and W. J. Himmel.** 1931. The environment of the prairie. Cons. and Surv. Div. Univ. Nebr. Bull. **5:** 1-50.

———**, V. H. Hougen and M. D. Weldon.** 1935. Relation of root distribution to organic matter in prairie. Bot. Gaz., **96:** 389-420.